9. The role of termites in ecosystems

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The role of any organism in an ecosystem can be defined in terms of three essential features. The first expresses its ability to divert a proportion of the total energy flow through the ecosystem towards increasing its own production. The second is its influence on the physical structure of its environment, and the third is its interaction with other organisms. When assessing the role of particular groups of organisms such as termites, a different aspect of populations, species diversity, must also be considered.

The first feature relates to the density and dynamics of populations and biological factors such as predation that affect their growth. It involves the various parameters of specific energetics, namely food collection, consumption and utilisation. It is apparent from earlier chapters that as far as termites are concerned, the study is in its infancy, and so little is known that the value of a synoptic and synthetic treatment of this field of research may be questionable. Recent work, only now gradually being published, has begun to remedy this deficiency. Noteworthy in this respect are the following projects within the IBP: derived savannah in the Ivory Coast (Josens, 1971*b*, 1972); Sahelian savannah in Senegal (Lepage, 1972, 1974*b*); semi-arid desert in USA (Haverty, 1974; Haverty & Nutting, 1975); tropical rainforest in Malaysia (Matsumoto, 1976). Ecological studies in natural and agricultural ecosystems in southern Guinea savannah in Nigeria by a research team (T. G. Wood, R. A. Johnson, C. E. Ohiagu, and N. M. Collins) organised jointly by the Centre for Overseas Pest Research and Ahmadu Bello University (COPR/ABU) (Wood, Johnson & Ohiagu, 1977) are also providing relevant information.

The second feature is one in which social insects in general and termites in particular have a greater impact than many more conspicuous organisms. They construct extensive and often massive nest systems in response to their need for food, environmental control and social homeostasis. As a result, they have a profound effect on redistribution of soil particles, on physical and chemical properties of soils, and consequently, on vegetation. A little is known of the extent of these modifications of the habitat, but the interactions within the termite–soil–vegetation system are complex and are nowhere fully understood.

Interaction with other organisms by termites involves a variety of direct and indirect effects, some of which are mentioned above; others include

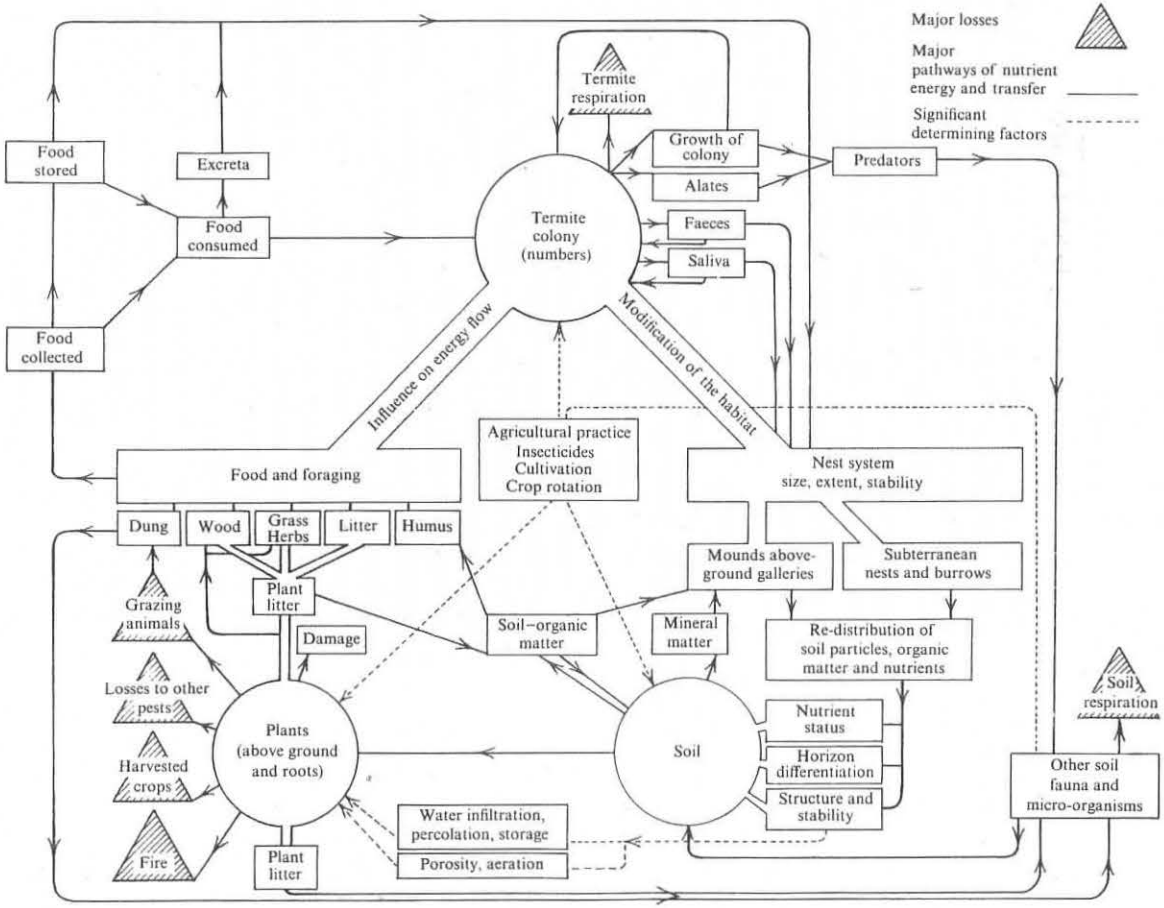

Fig. 9.1. Diagrammatic representation of role of termites in ecosystems showing the two major effects of termite communities: direct and indirect modification of the habitat by construction of nest systems and effects on energy flow and nutrient cycling by consumption and transformation of food (modified from Wood, 1975).

symbiotic and commensal relationships. These have resulted in mutual adaptations at several levels of intensity, but have never been quantified.

The role of termites in ecosystems can be usefully summarised pictorially as in Fig. 9.1. This distorts the true situation which is obviously not as termite-centred as shown in the model. However, it provides a framework for discussion and clearly illustrates the two major aspects of their role, modification of the habitat, and contribution to energy flow and the cycling of nutrients.

The order of importance, assigned above to the essential features of their ecological role, is not the most convenient arrangement for the more detailed account that follows. Here, we have first dealt with the zoogeographical aspect of species diversity, followed by the environmental effects of termites, and finally with their influence on energy flow, incorporating direct interactions with other organisms.

Diversity of species

Most termites are tropical or sub-tropical, though a few species extend into temperate regions as far as 45° N and S latitude. Roughly two-thirds of the world's land surfaces therefore, have one or more termite species. If one uses the simplest measure of species diversity, number of species per unit area, there is for most groups of animals and plants a tendency for species diversity to increase with proximity to the equator and to decrease with increasing altitude. Termites conform to this pattern, as illustrated by data from West Africa (Table 9.1); although the intensity of collecting and the area searched was not constant in the five localities there is an obvious north to south increase in the number of species. Similar trends can be discerned in the data of Harris (1961), Kemp (1955), and Sen-Sarma (1974).

The apparent exception to this general rule occurs in Australia (Gay & Calaby, 1970) where there are equal numbers of species north and south of the tropic of Capricorn, and few species in tropical rainforest. There are several peculiarities about the Australian fauna that suggest a zoogeographical rather than an ecological explanation, such as the lack of soil-feeding termites (Lee & Wood, 1971*b*), the presence of the primitive relic *Mastotermes darwiniensis* Froggatt (Mastotermitidae) and the absence of the fungus-growing Macrotermitinae.

Species lists for individual ecosystems are scarce. In addition to the data in Table 9.1, which are from localities within the tropics, there is Nutting's (unpublished) list of eight species in semi-arid shrubland (31.5° N) in Arizona and Lee & Wood's (1971*b*) list of nine species in warm temperate woodland (35° S) in south Australia. There are lists for larger (Krishna & Weesner, 1970) or more localised (Kemp, 1955; Roy-Noel, 1974) geo-

Table 9.1. *Number of species of termites and their feeding habits in different ecosystems in West Africa*

Locality	Latitude (N)	Total number of species	Living wood and fresh, woody litter	Grass and herbaceous litter	Decomposing wood	Soil
Sahel savannah, Senegal[a]	16.5°	19	11	8	0	3
Northern Guinea savannah, Nigeria[b]	11°	19	9	11	1	5
Southern Guinea savannah, Nigeria[c]	9°	23	10	10	2	8
'Derived' savannah, Ivory Coast[d]	6°	36	18	11	3	13
Rain forest, Cameroun[e]	4.5°	43	8	2	8	31

[a] Lepage (1972). Total area: 100 hectares.
[b] Sands (1965*a*). Area 1. Total area: 4 hectares.
[c] Wood, Johnson & Ohiagu (1977). Including primary and secondary savannah woodland. Total area: 7 hectares.
[d] Josens (1972). Including sparsely wooded and densely wooded savannah. Total area: 2700 hectares, but not including other vegetation types within this area.
[e] N. M. Collins (personal communication). Total area: 1.5 hectares.

graphical areas but these lists incorporate data from several different ecosystems.

It is obvious that there are relatively few species of termites, compared with the majority of invertebrates, including other social insects. Species diversity in general is often directly correlated with the biological stability of ecosystems, although opinions differ as to whether or not the relationship is causal (May, 1973; van Emden & Williams, 1974; Goodman, 1975). Diversity and biological stability may become mutually reinforcing phenomena as an end-point of evolution in physically undisturbed ecosystems; however, in the early stages of speciation, adaptive changes are more likely to be imposed by instability. Intricate habitat partitioning would appear to require a combination of rapid selection of adaptive features and mechanisms having potential for genetic isolation. These commonly take the form of courtship patterns, sexual recognition pheromones, or elaborate copulatory apparatus.

Termites have no sclerotised genitalia, and the evidence now accumulating suggests that sex pheromones may have little specific significance; courtship is minimal. Such fossils as exist are closely related to extant forms, showing little change over many millions of years. The relative longevity of most termite colonies, combined with a low success rate for the establishment of new ones, could explain their apparently slow evolution. With their internally controlled environmental homeostasis,

generalised feeding habits, rather large colony biomass and efficient digestion, termites in some ways resemble vertebrate primary consumers. It is evident that their impact on ecosystems arises from their numerical abundance and elaborate behaviour patterns rather than through species diversity.

Modification of the habitat

Termite nest systems and their composition

Termite nest systems may be arboreal, either within or attached to the outside of the vegetation, epigeal (the well-known mounds), or subterranean. They consist of one or more breeding centres from which radiate a network of galleries or runways to requisites such as food, water and soil (see Chapter 4, this volume).

The nests and associated galleries and runways are constructed from soil, excreta and saliva in varying proportions. Lee & Wood (1971*b*) recognised four main types of structure based on the materials from which they are composed, as shown by microscopical examination of thin sections.

(1) Fabrics dominated by re-packed orally transported soil particles without admixture of excreta.

(2) As (1), but incorporating excreta.

(*a*) Wood-feeders.

(*b*) Grass-feeders.

(3) Fabrics dominated by excreta consisting of soil (i.e. from soil-feeding species) mixed with orally transported soil particles.

(4) Fabrics dominated by excreta consisting of organic matter derived from ingestion of plant material.

(*a*) Wood-feeders.

(*b*) Grass-feeders.

The first category, in which soil particles are cemented solely with saliva, includes the large mounds of Macrotermitinae that form a conspicuous feature of many landscapes in Africa and Indo-Malaya. The second category includes the hard, outer crusts of mounds of several other groups (Termitinae, Nasutitermitinae and also in Australia, *Coptotermes*) in which excreta is used, in addition to saliva, in varying proportions as a cementing medium, and particularly the inner regions of the nests of these species in which greater proportions of excreta are often incorporated as distinct linings of chambers and galleries. The third category includes the nests of soil-feeders and their composition therefore reflects both the feeding habits of the species concerned (about which little is known, see Chapter 4, this volume) and the extent to which orally transported soil particles are incorporated into the nest structures. The fourth category includes concentrations of faeces derived from extensively digested plant material,

Table 9.2. *Particle size analysis, organic carbon (%) and nitrogen (%) content of constructions made by termites in which soil is the dominant constituent (fabric types 1, 2 and 3, see text)*

Species no. in Fig. 9.2.	Type of fabric and species of termite	Type of construction and soil depth (cm)	Coarse sand	Fine sand	Silt	Clay	Organic carbon	Nitrogen
	Fabric type 1							
1	*Macrotermes*	Mound, external wall	46	11	8	33	0.8	—
2	*bellicosus*[a]	Mound internal	16	17	9	58	0.9	—
		Soil, 0–15	68	13	5	7	0.5	—
		30–76[g]	48	10	7	35	0.3	—
3	*M. bellicosus*[b]	Mound, external wall	10	62	2	26	0.2	—
4		Mound, internal	9	60	1	30	0.5	—
		Soil, 0–15	11	62	2	25	1.2	—
		49–95[g]	10	62	3	25	0.2	—
5	*Macrotermes*	Mound, external wall	15	11		(73)	0.6	0.06
	subhyalinus[c]	Soil, 0–10	38	30		(32)	2.6	0.26
		67–70[g]	49	31		(20)	0.5	0.25
6	*M. bellicosus*[d]	Mound, external wall	—	—	—	—	0.5	0.09
7		Runways, over tree	—	—	—	—	1.4	0.14
8	*Odontotermes* sp.	Runways, over tree	—	—	—	—	0.7	0.09
9	*Ancistrotermes* sp.	Runways, over tree	—	—	—	—	1.2	0.15
		Soil, 0–5	—	—	—	—	0.9	0.08
		75–100[g]	—	—	—	—	0.4	0.07
10	*Odontotermes*	Mound	18	19	9	44	1.0	0.13
	redemanni[e]	Topsoil	19	20	8	43	2.0	0.18
11	*O. redemanni*[e]	Mound	39	38	4	15	0.9	0.10
		Topsoil	54	39	1	6	0.7	0.08
12	*Odontotermes*	Mound	34	37	5	19	1.2	0.08
	obscuriceps[e]	Topsoil	34	34	4	23	0.7	0.05
	Fabric type 2 (*a*) Wood-feeders							
13	*Coptotermes*	Mound, external wall	21	41	5	31	2.7	0.08
	acinaciformis[f]	Soil, 0–25	31	46	6	16	3.4	0.17
		60–75[g]	34	43	3	21	0.2	0.01
14	*C. acinaciformis*[f]	Mound, external wall	11	39	20	25	2.4	0.10
		Soil, 0–10	18	56	21	5	0.5	0.04
		20–40[g]	10	37	24	28	0.4	0.04
15	*C. acinaciformis*[f]	Mound, external wall[1]	6	17	22	53	2.7	0.09
16		Galleries, within wood[2]	5	9	15	69	2.8	0.06
		Soil, 0–10[1, g]	8	18	24	53	2.1	0.12
		30–40[2, g]	5	10	15	71	0.6	0.05
17	*Nasutitermes*	Mound, external wall	23	37	5	33	4.0	0.10
	exitiosus[f]	Soil, 0–12	37	49	7	7	1.0	0.08
		25–30[g]	19	27	3	49	0.5	0.04
18	*N. exitiosus*[f]	Mound, external wall	26	31	9	30	2.8	0.10
19	*Coptotermes lacteus*	Mound, external wall	16	26	7	47	2.4	0.08
		Soil, 0–20	35	47	10	9	1.6	0.10
		55–70[g]	24	28	9	40	0.3	0.40
20	*Schedorhinotermes*	Galleries, over log	6	10	18	61	7.4	0.16
	intermedius	Soil, 0–10	8	18	24	53	2.1	0.12
	actuosus[f]	30–50[g]	5	10	15	71	0.6	0.05
21	*Amitermes*	Mound, external wall	24	12		(64)	4.2	0.22
	unidentatus[c]	Top soil	22	19		(59)	2.3	0.25
22	*Nasutitermes*	Epigeal, external wall	35	25		(40)	2.3	0.33
23	*latifrons*[c]	Epigeal, internal	15	30		(55)	2.3	0.33
		Topsoil	44	33		(23)	2.1	0.14

Table 9.2 (*cont.*)

Species no. in Fig. 9.2.	Type of fabric and species of termite	Type of construction and soil depth (cm)	Coarse sand	Fine sand	Silt	Clay	Organic carbon	Nitrogen
	(*b*) Grass-feeders							
24	*Nasutitermes triodiae*[f]	Mound, external wall	18	41	12	25	2.7	0.10
25		Mound, internal base	13	46	12	23	2.5	0.11
		Soil, 0–6	23	24	14	9	0.5	0.04
		40–50[g]	20	45	14	18	0.2	0.02
26	*Amitermes laurensis*[f]	Mound, external wall	14	44	4	34	2.1	0.19
27		Mound, internal	19	49	9	24	1.3	0.11
		Soil, 0–20	26	65	4	4	0.5	0.04
		45–60[g]	27	40	7	24	0.3	0.03
28	*A. laurensis*[f]	Mound, external wall	7	41	27	19	3.0	0.16
29		Mound, internal	6	42	29	20	1.5	0.10
		Soil, 0–8	7	43	37	9	0.9	0.07
		16–24[g]	7	28	23	40	0.2	0.02
	Drepanotermes rubriceps[f]	Subterranean 0–5	22	52	9	14	1.4	0.12
		nest, 5–30	24	52	8	14	0.6	0.05
		Soil, 0–30[g]	25	52	8	14	0.9	0.08
		30–60	26	54	6	14	0.2	0.03
30	*D. rubiceps*[f]	Mound, external wall	14	59	3	20	1.4	0.09
31		Mound, internal	15	60	5	20	1.1	0.07
		Soil, 0–10	19	65	4	9	0.5	0.03
		20–30[g]	17	63	2	16	0.2	0.02
32	*Trinervitermes geminatus*[d]	Mound	—	—	—	—	1.4	0.08
		Soil, 0–5	—	—	—	—	0.9	0.08
		75–100	—	—	—	—	0.5	0.07
	Fabric type 3							
33	*Cubitermes sankurensis*[b]	Mound	6	41	14	39	3.8	—
		Soil, 0–12[g]	13	64	3	20	2.8	—
		30–50[g]	11	66	2	21	0.7	—
34	*Cubitermes fungifaber*[c]	Mound	13	41	(46)		1.4	0.11
		Soil, 0–5[g]	30	45	(25)		1.1	0.08
		60[g]	23	49	(27)		0.3	0.03
35	*Cubitermes* sp.[d]	Mound	—	—	—	—	1.4	0.08
		Soil, 0–5	—	—	—	—	0.9	0.08
		75–100	—	—	—	—	0.5	0.07

[a] Nye (1955).
[b] Stoops (1964).
[c] Maldague (1959).
[d] Wood (unpublished data from Nigerian savannah).
[e] Joachim & Kandiah (1940).
[f] Lee & Wood (1971*a*).
[g] Suspected or proven soil horizon used by termites for building.

collectively known as carton. These structures form the greater part of the arboreal type of nest of certain Termitinae and Nasutitermitinae and certain inner regions of the nests of *Mastotermes* and some Hodotermitidae, Rhinotermitidae, Amitermitinae and Nasutitermitinae. The nests of Macrotermitinae are unique in that all excreta are used to construct fungus combs; these structures are not regarded as carton, as the excreta consist of plant material which has undergone little chemical change.

Details of these fabrics are given in Lee & Wood (1971*b*) except for those of soil-feeders for which information is based solely on *Cubitermes* (Stoops, 1964). More detailed micro-pedological features are discussed by

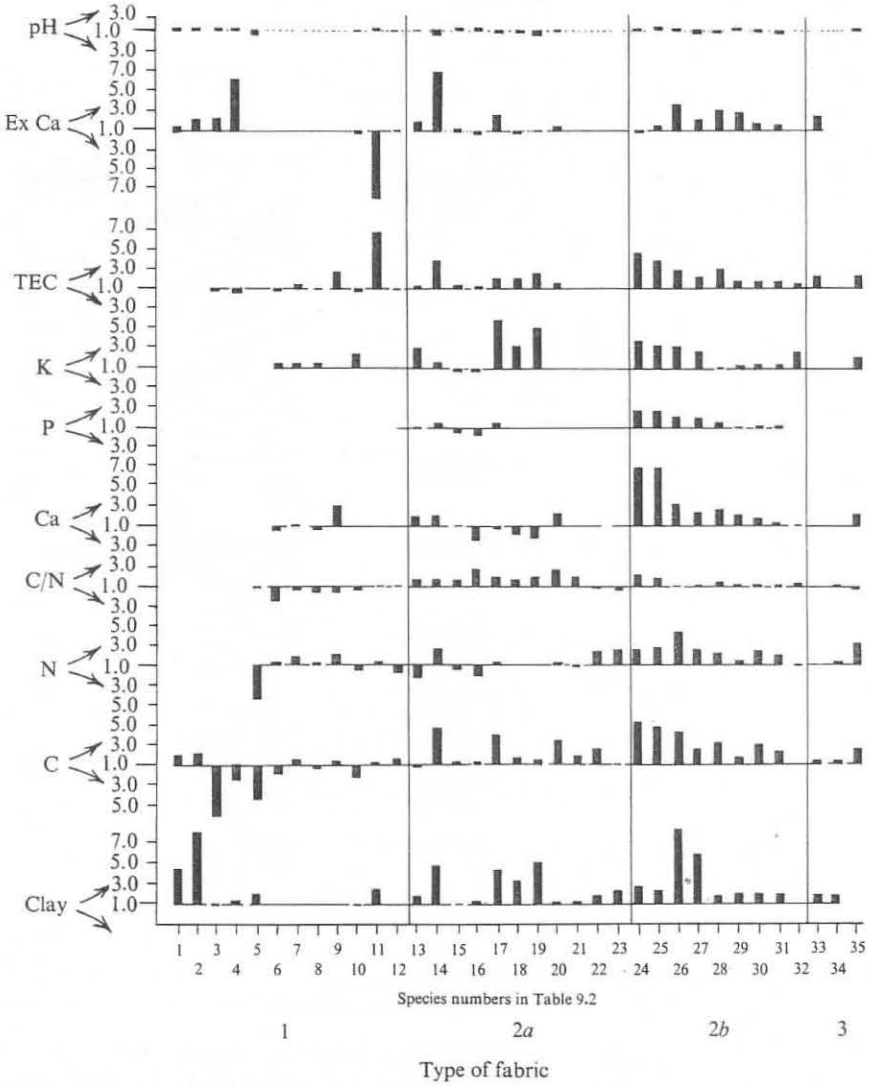

Fig. 9.2. Comparison of the clay, carbon (C), pH and nutrient content of constructions, in which soil is the dominant constituent, made by termites and topsoil of the adjacent soil. Histograms above the base line of 1.0 indicate termite construction contains 2.0, 3.0, etc. times the amount in soil; histograms below base line indicate soil contains 2.0, 3.0, etc. times the amount in termite structure. Termite structures correspond to those listed in Table 9.2 except for the subterranean nest of *Drepanotermes* which is excluded from the figure. For explanation of type of fabric see text. (P = phosphorus, K = potassium, Ca = calcium, Ex Ca = exchangeable calcium, N = nitrogen, TEC = total exchangeable cations.)

Sleeman & Brewer (1972). Physical and chemical analyses of a selection of these structures are given in Tables 9.2 and 9.3 and Fig. 9.2.

The construction of these greatly diverse nest systems results in the transport of soil from either deep or shallow horizons (often from both) to the soil surface where it is formed into mounds, covered runways or sheetings on the soil surface and over, or within, vegetation on which the termites are feeding. There is a concurrent construction of a network of subterranean galleries and the removal of food from the foraging territory of the colony with consequent incorporation of the end-products of digestion (excreta) into various structures of the nest system. The effects of these processes on modification of the habitat can be considered in relation to soils and vegetation separately, although the influence on vegetation (apart from feeding which is discussed elsewhere) is largely indirect and is brought about by modification of soils.

Modification of soils

The effects of termites on soils has been reviewed by Lee & Wood (1971*b*) and since this publication there have been few studies which either provide comparable information or illuminate the deficiencies in present knowledge indicated by this review. These authors indicated that studies had concentrated on the more obvious effects of mound-building species whereas the effects of subterranean species may be equally significant. Recent work, as yet unpublished, confirms this suggestion.

Modifications to soils can be considered under the following headings:

(i) physical disturbance of soil profiles;
(ii) changes in soil texture;
(iii) changes in the nature and distribution of organic matter;
(iv) changes in the distribution of plant nutrients;
(v) construction of subterranean galleries.

Physical disturbance of soil profiles

The modification of soil profiles as a result of termite activity depends on the fact that termites remove soil from various depths and bring it to the surface in the form of runways, sheetings or mounds from which it is re-distributed by water and wind erosion. Some of this material is re-distributed on the soil surface, some is carried away in rivers. These processes were noticed as long ago as the last century by Drummond (1888) who remarked on how Herodotus had described Egypt as the 'gift of the Nile', but that '. . . had he lived today he might have carried his vision farther back still and referred some of it to the labours of the humble termites in the forest slopes about Victoria Nyanza'.

The amount of soil in mounds and the area of ground covered by them

was summarised by Lee & Wood (1971*b*). The weight varies from less than 10000 kg per hectare for small mounds of less abundant species to 45000 kg per hectare for small mounds of more abundant species; large mounds of *Macrotermes* in Africa may contain from $1–24\times10^5$ kg per hectare of soil, the maximum equivalent to a uniform layer 20 cm deep being found in one particular area in the Congo (Meyer, 1960). The percentage of land area occupied likewise varies from less than 1.0% up to 30% in the case of the *Macrotermes* mentioned above. Comparable information for the amount of soil in runways, surface sheetings and in-filled vegetation is not available except for certain unpublished information. Preliminary measurements in southern Guinea savannah woodland in Nigeria of the amount of soil in the form of sheeting constructed by Macrotermitinae (largely *Macrotermes bellicosus* (Smeathman) and species of *Odontotermes*, *Ancistrotermes* and *Microtermes*) on trunks and branches of trees was estimated at 300 kg per hectare and in an entirely different ecological situation, a maize field on the same soil type, the amount of soil carried up within the stems of maize plants attacked by *Microtermes* was estimated at 250 kg per hectare. Lepage (1974*b*) estimated that the soil-surface runways and sheetings of *Macrotermes subhyalinus* (Rambur) in Sahel savannah in Senegal amounted to 675–950 kg per hectare.

There are few measurements of the rate of erosion of soil from termite mounds and its accumulation on the soil surface. In northern Australia Williams (1968) estimated that mound-building termites (*Tumulitermes hastilis* (Froggatt), *Tumulitermes pastinator* (Hill) and *Nasutitermes triodiae* (Froggatt)) had brought 6000 m^3 per hectare of soil to the surface. Of this, 1500 m^3 per hectare remained to form a layer 15 cm deep which had formed over a period of 12000 years giving a rate of accumulation of 0.0125 mm per year; 4500 m^3 per hectare had been removed by erosion. In two other localities in northern Australia where the mound-building termites were *T. hastilis*, *N. triodiae*, *Amitermes vitiosus* Hill and *Drepanotermes rubriceps* (Froggatt), Lee & Wood (1971*b*) calculated accumulation rates of 0.02 to 0.10 mm per year. These rates are of a similar order of magnitude to that of 0.025 mm per year calculated by Nye (1955) as resulting from erosion of mounds of *Macrotermes bellicosus* in West African forest. Pomeroy (1976*a*) estimated rates of erosion from mounds of *M. bellicosus* and *Pseudacanthotermes* spp. in Uganda to be 1.3 m^3 per hectare per year, equivalent to a layer 0.13 mm deep, some of which would accumulate on the surface and some of which would be lost. A contributory factor in erosion was destruction of mounds by man to the extent that losses by erosion exceeded gains from construction by a factor of one-third which indicated that mounds would cease to exist in approximately 100 years. These rates may seem slow and over the lifetime

of a single mound (which may approach 100 years in the case of large mounds of *Macrotermes* in Africa and *Nasutitermes triodiae* in Australia) eroded soil is not spread evenly but accumulates around the base of the mound. However, on ancient landscapes several thousand years old these irregularities become evened out to the extent that soil derived from termite mounds forms distinct surface horizons. Williams (1968) observed that in northern Australia, stone lines were buried under a depth of 15 cm of such material, and comparable observations by Fölster (1964), Nye (1955), Ollier (1959), de Ploey (1964) and Stoops (1968) indicate that this is a feature common to many tropical soils in both forest and savannah regions. This subject is discussed in more detail by Lee & Wood (1971*b*).

Erosion of soil sheetings on vegetation and runways and sheetings on the soil surface has not received the attention it deserves. Lepage (1974*b*) showed that of the 2000 kg per hectare of soil brought to the surface every year by *Macrotermes subhyalinus* in Senegal, between 675 and 950 kg per hectare was in the form of foraging runways and sheetings on the soil surface. Observations show that these fragile structures are rapidly eroded by rain and are just as rapidly re-built, but rates of accumulation and removal have not been measured. In mechanically cultivated agricultural ecosystems where mounds are destroyed, soil is brought to the surface by termites solely in the form of foraging galleries and runways. Measurements in southern Guinea savannah in Nigeria show that *Microtermes* populations attacking maize (Wood *et al.*, 1977) bring 250 kg per hectare of subsoil to the surface where it is re-packed within the eaten out stems of the maize plants and is re-distributed by subsequent cultivation.

In the soils of some dry regions where laterite outcrops occupy much of the ground surface, soil eroded from termite mounds and other structures may eventually bury the laterite crusts (Grassé, 1950; Tricart, 1957; Boyer, 1959). Herbaceous vegetation colonises cracks or pockets containing soil particles and is eventually followed by shrubs and trees; the laterite finally disintegrates (or under humid conditions may disappear altogether) forming a gravelly soil (Maignien, 1966). Thus termites contribute to the modification and degradation of laterite. However, after considering the evidence presented by several authors who had suggested that the abandoned galleries and nests of termites serve as sites for the formation of certain forms of laterite, Grassé & Noirot (1959*a*) and Lee & Wood (1971*b*) concluded that it is most unlikely that laterite is formed from these structures.

Abandoned subterranean galleries and nests are often filled with soil washed in from the surface. These have been observed by several authors, such as Watson (1960) who observed in-filled galleries at depths of 8.5 m, but the extent and rate of the process has never been measured.

Changes in soil texture

The significance of the physical disturbance of soil profiles depends partly on the nature of the soil brought to the surface by the termites and partly on physical and chemical changes in the soil due to the activities of the termites. Chemical changes are brought about by incorporation of organic matter and are discussed below. Physical changes appear to be due to selection and sorting of certain particles resulting in a change of structure and particle size distribution. The only instance of production of fine particles from coarse ones by termites is Boyer's (1948) claim that *Macrotermes subhyalinus* occasionally work particles of mica in their mandibles until the material has properties similar to illite and can be used in the construction of mounds as a substitute for naturally-occurring clay.

Particle size analyses of mounds and other structures made by termites and of surrounding soils have been carried out by several workers and Lee & Wood (1971*b*) summarised and discussed these along with their own data (Lee & Wood, 1971*a*) for Australian termites. A representative selection of analyses is shown in Table 9.2. By analysing clay minerals in the mounds and different soil horizons Lee & Wood (1971*a*) showed that for the 12 species they studied in 17 different localities 15 mounds were derived entirely from subsoil, six entirely from topsoil and 10 from both topsoil and subsoil.

Obviously pedological changes resulting from redistribution of mound material are greater if subsoil is used in preference to topsoil. Selection of subsoil rich in clay is a feature of the building behaviour of many Macrotermitinae (Table 9.2 and Fig. 9.2). Analyses of mounds of *Macrotermes* (Hesse, 1955; Nye, 1955; Maldague, 1959; Stoops, 1964; Pomeroy, 1976*b*) illustrate selection for clay but in soils with an extremely high clay content there may be preferential selection of sand particles although the mound is constructed primarily from clay. The present authors' observations in southern Guinea Savannah at Mokwa, Nigeria indicate that mound-building and non-mound-building Macrotermitinae often select clay subsoil for constructing runways and sheets on the outside of trees or on the soil surface (e.g. *Macrotermes*, *Odontotermes* and *Ancistrotermes*) or for filling-in galleries within eaten-out branches, and twigs (the above species plus *Microtermes*).

Most mound-building termites are less selective than the Macrotermitinae and build mounds with a wide range of textures (e.g. *Coptotermes acinaciformis* (Froggatt), Table 9.2). Generally there is selection for clay-sized particles in preference to sand with the result that mounds tend to have a higher content of clay than the soil from which they are constructed. Mounds are constructed entirely from materials transported by the termites whereas subterranean nests are constructed either from transported

material or simply by excavating and re-packing the soil *in situ*. An example of the latter is the subterranean nest of *Drepanotermes rubriceps* (Table 9.2) whereas an outstanding example of selection are the subterranean nests of the soil-feeding *Apicotermes* which constantly consist of 81–83% fine sand (Stumper, 1923).

The changes in texture brought about by the re-distribution of mounds and other structures on the surface is likely to be accompanied by changes in physical properties, such as structure, stability, bulk density, infiltration rate, permeability and water-holding capacity. However, with the exception of Macrotermitinae, which do not use their excreta for building purposes, changes in these properties will also be influenced by excreted organic matter incorporated into the various structures. There is some evidence that aggregates from termite-modified soil are more stable than those from undisturbed soil particularly if the aggregates contain organic matter (excreta) in which case they may even resist chemical dispersion (Lee & Wood, 1971*b*). There are very few measurements of other physical properties of termite-modified soil resulting from changes in soil texture and these were reviewed by Lee & Wood (1971*b*).

Changes in the nature and distribution of organic matter

The chemical changes in food material brought about during digestion are discussed in Chapters 4 and 7 of this volume. Here we are concerned solely with effects of collection and utilisation of food on the distribution of organic matter in the ecosystem and the effects of the chemical transformations on the subsequent fate of excreted organic matter. It is apparent from Chapter 4 that plant material, in whatever form it is consumed (wood, grass, soil, etc.), once collected by foraging termites is largely utilised in the region of the central nest system housing the queen and young termites. Unlike other soil animals which deposit faeces within the soil where they are available to micro-organisms and coprophagous invertebrates, termites use their excreta to construct certain regions of the nest (e.g. nursery chamber, linings of gallery walls) or, in the case of Macrotermitinae, fungus combs which are further utilised as food. Thus organic material and the nutrients it contains are collected from a wide area and concentrated largely in the central region of the nest system.

The use of salivary secretions and faeces in building mounds and runways raises their organic content above that of the soil from which they are derived (Table 9.2 and Fig. 9.2). However, mounds are often built from subsoil, and even when modified by termites this remains lower in organic matter than the surrounding topsoils. This is generally true of mounds built by Macrotermitinae though few analyses are available (Table 9.2) for constructions other than mounds (i.e. surface runways, mud-fillings in excavated food sources, etc.).

In addition to being re-distributed, organic matter is profoundly changed during its passage through the termite's gut and ultimately one of the more important effects is a change in the carbon/nitrogen (C/N) ratio. Lee & Wood (1971*a*) showed that for 30 samples of termite-modified soil in Australia all except two samples showed an increase in the C/N ratio compared with adjacent soil. The C/N ratio expressed as a factor of the C/N ratio of corresponding soil samples was 0.8–2.0 (mean 1.4) for grass-eating termites and 1.1–2.7 (mean 1.9) for wood-eating termites. Thus erosion of these structures and re-distribution of termite-modified soil over the soil surface results in the addition of organic matter of a relatively high C/N ratio (up to 47). In contrast, mounds and other structures of Macrotermitinae in Africa (Boyer, 1955; Pomeroy, 1976*b*) and Asia (Joachim & Kandiah, 1940; Shrikhande & Pathak, 1948) appear to have C/N ratios similar to or even lower than adjacent soil (Table 9.2, Fig. 9.2), almost certainly a consequence of their behaviour in using subsoil for construction and not incorporating excreta as in the case of other species. Addition to the soil of organic matter of a high C/N ratio is in opposition to established processes of decomposition which, by the combined action of comminution of plant debris by soil-inhabiting invertebrates and microbial breakdown, reduce the C/N ratio of plant debris (25–40 for leafy tissues, 50–80 for woody tissues) to values of 10–15 found in soil humus.

This increase in the C/N values of termite-modified soil is even more obvious when analytical data for carton and other structures made entirely or almost entirely from excreta are examined (Table 9.3). In Australia, Lee & Wood (1971*a*) obtained C/N values of 32–107 for wood-feeding species and 21–25 for grass-feeding species. A further relevant property of termite excreta is the high lignin/cellulose ratio compared with that of their food. Analyses of carton by Becker & Seifert (1962) and Lee & Wood (1971*a*) and of wood and excreta produced by wood-feeding termites by Seifert & Becker (1965) show that lignin/cellulose values of 0.38–0.82 in wood are drastically changed by the termites' digestive processes. Values ranged up to 15.7 for fresh excreta (excreta of *Reticulitermes lucifugus* var. *santonensis* de Feytaud fed on *Pinus* with a lignin/cellulose value of 0.7) and up to 5.4 for carton. Returns of organic matter and nutrients to the ecosystem via the decomposition of faecal material is discussed later in this chapter and in Wood (1976).

Changes in chemical properties of soil and in the distribution of plant nutrients

The chemical properties of termite-modified soil in comparison with the soil from which it is derived can be attributed to differential selection of soil particles, incorporation of saliva, incorporation of excreta in the form

Table 9.3. *Chemical analysis of structures built by plant-feeding termites in which excreta is the dominant constituent (fabric type 4, see text). Nests as in Table 9.2. with addition of* Nasutitermes magnus *and* Tumulitermes pastinator

Termite species	Type of structure	pH	Carbon	Nitrogen	C/N[d]	Phosphorus	Calcium	Potassium
(*a*) Wood-feeders								
Macrotermes bellicosus[a]	Fungus comb, fresh	n.d.	31	0.68	46	0.07	0.70	0.10
	Fungus comb, old	n.d.	29	0.80	36	0.07	0.85	0.10
Odontotermes obscuriceps[b]	Fungus comb	n.d.	42	1.44	29	n.d.	n.d.	n.d.
Coptotermes acinaciformis[c]	Mound, carton wall	3.2	43	0.52	83	0.02	0.11	0.02
C. acinaciformis[c]	Mound, carton wall	3.2	43	0.67	64	0.02	0.17	0.11
	Mound, carton nursery	3.2	50	0.56	89	0.02	0.12	0.11
C. acinaciformis[c]	Mound, carton wall	3.1	44	0.41	107	0.02	0.30	0.05
Nasutitermes exitiosus[c]	Mound, carton wall	3.9	15	0.25	58	0.01	0.35	0.12
	Mound, carton nursery	3.9	30	0.52	58	0.02	0.52	0.07
N. exitiosus[c]	Mound, carton wall	4.0	29	0.51	57	0.03	0.11	0.23
	Mound, carton nursery	4.1	41	0.79	51	0.04	0.50	0.13
Coptotermes lacteus[c]	Mound, carton wall	3.9	29	0.45	65	0.02	0.31	0.21
	Mound, carton nursery	3.8	42	0.74	57	0.03	0.40	0.18
(*b*) Grass-feeders								
Nasutitermes triodiae[c]	Mound, carton nursery	5.6	10	0.44	23	0.03	0.22	0.28
Nasutitermes magnus[c]	Mound, carton nursery	4.9	19	0.73	26	0.03	0.18	0.23
Tumulitermes pastinator[c]	Mound, carton nursery	5.2	11	0.50	23	0.02	0.26	0.27

[a] Wood (unpublished data from Nigerian savannah).
[b] Joachim & Kandiah (1940).
[c] Lee & Wood (1971*a*).
[d] Carbon/nitrogen ratio.

of linings to gallery walls, gallery in-fillings, and in the case of the large mounds of Macrotermitinae, to pedological changes. Only a brief summary of the chemical differences between termite-modified soil and adjacent soils will be given here as this subject was discussed in detail by Lee & Wood (1971*a*, *b*).

pH

In mounds of Macrotermitinae there is generally a small increase in pH (often correlated with an increase in calcium, see below) compared with the subsoil from which the mounds are constructed but there is little difference compared with topsoil (Fig. 9.2). Structures made by other species generally have a lower pH (due to incorporation of organic-rich excreta) than subsoil but are similar to or only slightly lower than topsoil.

Carbon and nitrogen

In general there is a small increase in the abundance of these elements compared with subsoil, in mounds of Macrotermitinae, due to incorporation of saliva but the amounts involved are so low that often concentrations are lower than in topsoil (Fig. 9.2). Structures made by other species have higher concentrations due to incorporation of excreta and

as excreta has a high C/N ratio (Table 9.3) the C/N ratio of the termite-modified soil is correspondingly elevated.

Calcium

All termite-modified soils have higher concentrations of calcium than adjacent soils. In Macrotermitinae the increase has been attributed to several causes (Watson, 1974), but appears to be mainly due to the large evaporating surface of the mounds, often supplemented by an internal ventilation system which results in the accumulation of salts near the base of the mound. This phenomenon has been reported by several authors (e.g. Pendleton, 1941; Watson, 1962; Weir, 1973) and was studied in some detail by Hesse (1955) who showed that the process was accelerated by the presence of calcium-rich ground-water and by impeded drainage. These concentrations may be as high as 7% (Milne, 1947) resulting in calcium carbonate concretions amounting to 2000 kg per mound. These figures are exceptional and in many localities the calcium content of mounds is similar to or only slightly greater than that of the adjacent soil and is not in concretionary form, being distributed more or less evenly throughout the mound (Hesse, 1955; Nye, 1955; Pomeroy, 1976*b*; T. G. Wood, unpublished data from Nigeria). The increased calcium concentration in structures built by other termites is due to the incorporation of excreta.

Potassium

The concentration of potassium in termite-modified soil is usually higher than in subsoil due to the incorporation of organic matter in the form of excreta and/or saliva but may be slightly higher or slightly lower than in topsoil (Fig. 9.2).

Phosphorus

The relative concentrations of phosphorus in termite-modified soil, topsoil and subsoil are associated with relative levels of organic matter (see *Potassium*, above) but Hesse (1955) found that in large mounds of Macrotermitinae on sites with impeded drainage, phosphorus tended to accumulate at the base of the mound in the manner described for calcium.

Exchangeable cations

Addition of clay and organic matter (in the form of excreta and saliva) results in an increase in the total exchangeable cations (TEC) compared with adjacent soils and a significant proportion of this increase is due to an increase in exchangeable calcium (fig. 9.2; Lee & Wood, 1971*b*).

The general effects of these localised chemical changes on the properties of soils depend on the amount of termite-modified soil available and the rate at which it is re-distributed by erosion. The only relevant studies are

Table 9.4. *Addition of organic carbon and plant nutrients to soil surface as a result of erosion of termite mounds. For each site, figures are also given for the percentage by weight, and 'standing crop' (kg per hectare) of organic carbon and nutrients in the upper 10 cm of soil (bulk density of soil = 1.2)*

Locality and termite species	Annual erosion of mounds (kg per hectare)	Organic carbon		Nitrogen		Phosphorus		Potassium		Calcium	
		kg per hectare		kg per hectare		kg per hectare		kg per hectare		kg per hectare	
		(%)	per year	(%)	per year	(%)	per year	(%)	per year	(%)	per year
North Australia (site 4)[a]											
Nasutitermes triodiae	2310	2.6	60	0.10	2.3	0.01	0.2	0.07	1.6	0.22	5.1
Soil, 0–10 cm	—	0.5	6000	0.04	480	0.004	48	0.06	720	0.01	120
North Australia (site 6)[a]											
N. triodiae	150	2.6	4	0.10	0.2	0.01	< 0.1	0.07	0.1	0.22	0.3
Tumulitermes hastilis	10000	2.4	240	0.08	8.0	0.01	1.0	0.07	7.0	0.06	6.0
Amitermes vitiosus	2000	2.2	44	0.01	0.2	0.01	0.2	0.06	1.2	0.08	1.6
Drepanotermes rubiceps	2100	1.4	29	0.09	1.9	0.01	0.2	0.17	3.6	0.13	2.7
Total	14250	—	317	—	10.3	—	1.4	—	11.9	—	10.6
Soil, 0–10 cm	—	1.1	13200	0.06	720	0.014	168	0.06	720	0.06	720
Natete, Uganda[b]											
Macrotermes bellicosus	2300	—	—	0.064	1.5	0.0004	0.01	0.022	0.5	0.05	1.1
Pseudacanthotermes spp.	230	—	—	0.056	0.1	0.0006	< 0.01	0.020	0.1	0.06	0.1
Total	2530	—	—	—	1.6	—	0.01	—	0.6	—	1.2
Soil, 0–10 cm	—	—	—	0.07	840	0.0005	6	0.027	324	0.11	1320
Muko, Uganda[b]											
Macrotermes subhyalinus	8600	—	—	0.091	7.9	0.0017	0.15	0.03	2.5	0.09	9.1
Soil, 0–10 cm	—	—	—	0.10	1200	0.001	12	0.01	120	0.06	720

[a] Calculated from data in Lee & Wood (1971*a*) assuming that rate of erosion of occupied mounds is similar to that of abandoned mounds.
[b] Calculated from data in Pomeroy (1976*a*, *b*).

those of Lee & Wood (1971*a*) in northern Australia and Pomeroy (1976*a*) in Uganda and some of these data are summarised in Table 9.4. In northern Australia the mounds were built by various grass-feeding termites which incorporate excreta into their mounds. In the two localities taken as examples, the weight of various elements eroded annually from mounds, as a percentage of their weight in the upper 10 cm of soil, amounted to: carbon (1.0–2.4%), nitrogen (0.7–1.4%), phosphorus (0.4–0.8%), potassium (0.2–1.7%) and calcium (1.5–4.3%). In Uganda the mounds were built by various Macrotermitinae and the corresponding percentages were: nitrogen (0.2–0.7%), phosphorus (0.2–1.3%), potass-

ium (0.2–2.1%) and calcium (0.1–1.1%). However, an unknown proportion of these elements will be lost through drainage and surface run-off so that their contribution to the nutrient status of the surface soil will be less than indicated.

Little is known about the decomposition of structures composed largely of excreta (carton) but in the case of *Nasutitermes exitiosus* (Hill) these structures appear to persist until burnt by bushfires. Lee & Wood (1968) calculated that these structures contained 143 kg per hectare of nitrogen, 0.14 kg per hectare of phosphorus and 2.47 kg per hectare of calcium. On the assumption that mounds persist for 40 years and are then immediately eroded and the carton burnt the annual accession of elements is: nitrogen (0.53 kg per hectare, but much will be lost to the atmosphere by burning), phosphorus (0.004 kg per hectare) and potassium (0.062 kg per hectare).

From the above it is reasonable to conclude that erosion of termite mounds contributes very little to the nutrient status of soils; even if their contribution was doubled, to allow for erosion of runways and surface sheetings, their effect would be negligible compared with the accession of nutrients from decomposing plant material not attacked by termites, foliar leaching and rainwater. Erosion of structures built by Macrotermitinae often adds soil of a lower nitrogen content than topsoil.

Construction of subterranean galleries

The extent of foraging galleries was discussed in Chapter 4 of this volume and it was noted that they may extend up to 30 m from the central nest system. Galleries may also penetrate to great depths (presumably for the purposes of collecting water) and there are records (Lee & Wood, 1971*b*) of termites as deep as 70 m, although such depths are exceptional. The greatest concentration of galleries is found near the soil surface close to sources of food but there are no estimates of their dimensions, orientation or total extent, nor the length of time for which they persist once they have been abandoned.

These sub-surface termite galleries are commonly so numerous as to collapse under-foot, leaving deep imprints, as we and others studying the insects in the tropics have often observed. Heavy rains compact this spongy surface so that it largely disappears by the end of the wet season. Several workers (Adamson, 1943; Robinson, 1958; Maldague, 1964; Lee & Wood, 1971*b*) have commented on the fact that this dense network of galleries must affect porosity and aeration, infiltration, storage and drainage of water, and growth of plant roots, but these important effects have not yet been measured. Such measurements will be crucial to a proper understanding of the total influence of termites on soils.

Modification of vegetation

Termites can modify vegetation directly by consuming it and indirectly by influencing its growth on or around termitaria through modifications in soil properties. The direct effects of food consumption are discussed later in this chapter.

Influence of feeding activities

The removal of parts of a living plant for food often affects the growth and subsequent survival of the plant. Stimulation of growth has rarely been observed but an example is provided by Kaiser (1953). He showed that the nests of *Anoplotermes pacificus* Fr. Muller in Brazilian rainforest are invaded by a dense mat of plant roots (e.g. *Mapouria cephalantha* Muell.). The root apices are preferentially consumed by the termites, and the relationship appears to be symbiotic, as in abandoned termitaria the roots are dead. More often the effects of feeding on a particular part of a plant by termites result in loss in vigour, or in the death of the plant, but much will depend on the condition of the plant when attacked. For instance, grass is harvested by various species of termites in many tropical and semi-arid regions (Chapter 4, this volume). In normal years, grass growth may be sufficient to support all herbivores including termites, and vegetative growth may possibly be stimulated by cropping. During drought and heavy overgrazing by vertebrate consumers, the termites may kill the plants by taking or attempting to take their usual quota of food. This is because termites, unlike other primary consumers, are not limited by their accessibility to the aerial parts of the plant. There are no published measurements of these effects, but damage to plants in agriculture and forest plantations based on many observations was summarised by Harris, W. V. (1969) as follows:

(*a*) destruction of seedlings;

(*b*) ring barking, leading to death of the plant;

(*c*) destruction of root system often followed by tunnelling within stems, leading to wilting or lodging;

(*d*) removal of leaf tissue, resulting in loss of production and photosynthetic potential.

Influence through modification of soil properties

A resumé of this subject was given by Lee & Wood (1971*b*) who distinguished between growth of vegetation on termitaria and growth on termite-modified soil around termitaria.

The stimulation of plant growth on the mounds of certain Macrotermitinae in Africa and Asia, which often support a more luxuriant and woody vegetation than the surrounding scrub or savannah has been

recognised for many years. The difference may be so marked in some areas that distinct terms have been coined to describe the vegetation, such as 'termitensavannen' (Troll, 1936) or 'park-formation' (Fuller, 1915). Lee & Wood (1971*b*) summarised the more important factors responsible for enhancing growth on these termitaria as:

(*a*) protection from burning, allowing the survival of certain seedlings that would otherwise be destroyed by fire;

(*b*) improvement of drainage in areas subject to seasonal waterlogging;

(*c*) accumulation of a greater depth of soil in areas with shallow, stony soils;

(*d*) provision of moist soil in otherwise dry areas;

(*e*) producing chemically altered soil, chiefly by increasing pH and raising base-status;

(*f*) resistance to termite attack by species growing on the mounds;

(*g*) possible stimulation of growth (e.g. the case of *Anoplotermes pacificus* quoted above).

The large mounds of various Macrotermitinae in Africa and Asia appear to be the exception in supporting a distinct type of vegetation. Mounds of other species of termites (e.g. *Cubitermes*, *Trinervitermes*, *Amitermes* in Africa and *Coptotermes*, *Nasutitermes*, *Amitermes* in Australia) do not appear to support plant growth, even when abandoned by the termites. However, there are reports from South America (where Macrotermitinae do not occur) that vegetation similar to that of the surrounding savannah grows on abandoned mounds (Goodland, 1965: termites not identified) or that mounds (termites not identified and condition of mounds not indicated) support a distinct woody vegetation (i.e. having the appearance of 'termitensavannen') in contrast with the surrounding savannah (Smith, 1971).

Retardation of growth on termitaria is often regarded as being a direct effect of hardness, preventing infiltration of water and establishment of seedlings (Glover *et al.*, 1964; Watson & Gay, 1970). It may also be due to the presence of toxic substances in the termites' excreta (Lee & Wood, 1971*b*).

Distinct patterns in the growth of vegetation around termitaria have also been recorded. Frequently these observations relate to the lack of plant growth on the areas of surrounding soil eroded from termite mounds (Macfadyen, 1950; Glover *et al.*, 1964; Lee & Wood, 1971*b*). When these areas are colonised, it is by plants normally associated with hardpans (Burtt, 1942; Glover *et al.*, 1964). A more detailed study of vegetation growing around mounds of *Odontotermes* sp. in Kenya was made by Glover *et al.* (1964), who suggested that the differential growth was due to response by the plants to variations in soil moisture and amounts of clay and salts washed off the mounds and moved downslope by water.

Effects of modification of habitat on fauna

The intimate relationships of lestobiosis, termitophily and similar phenomena existing between termites and other organisms is discussed later in this chapter. There are many less intimate, often casual or even fortuitous, relationships between termite nest systems and other organisms which Berg (1900) described under the general term of 'termitariophily'. Araujo (1970) wrote 'Termite nests provide an alluring biotope for a great assemblage of organisms, yet although extensive lists could be compiled the nature of these associations is poorly understood in most cases.' This author provided many examples of mammals, birds, reptiles, amphibians and invertebrates using termitaria as vantage points, nesting sites or for shelter. None of these associations appeared to be obligatory but Lee & Wood (1971*b*) reported on the apparently obligatory nesting behaviour of certain species of Australian parrots which excavate and nest in holes in the sides of termite mounds.

The effects of termitaria on vegetation, for instance, in preserving or developing small areas of forest in derived or natural savannahs, must have an indirect effect on the distribution of many other animals. It is well known that the clumps of trees growing on termite mounds of one or more species provide an environment for forest-limited members of other termite genera in Africa, South America and the Orient. The same must be true for many other groups of invertebrates and possibly some vertebrates but there is little information and this is undoubtedly a rich field for further ecological study.

The accumulation of salts in the large mounds of *Macrotermes* are occasionally exploited as salt licks by elephants (Weir, 1972) and possibly by other animals, but this is not a general phenomenon and is probably resorted to only when more readily accessible salt is unavailable.

Population energetics and interactions with other organisms

Energetics of individual species

Energy flow through a population is described by the following equations:

$$C = A + F \tag{9.1}$$

$$A = P + R \tag{9.2}$$

where C = consumption, P = production, R = respiration, A = assimilation and F = faeces production. Measurements of some of these parameters are available only for a few individual species of termites. They can be combined with estimates of population density to assess energy flow through termite communities and the means by which nutrients are returned to the ecosystem.

Population density

Attempts to sample termite populations quantitatively encounter two main problems. Their social behaviour makes termites more discontinuously distributed than non-social insects and most species have subterranean nests that may penetrate the soil to depths of several metres.

Sampling problems and methods were reviewed by Lee & Wood (1971*b*) and Sands (1972*b*), both of whom pointed out that figures for abundance were notably confined to individual mound-building species. Until recently, there had been no quantitative estimate of the entire termite community in any ecosystem but three separate attempts have now been made in different West African savannahs. Lepage (1972, 1974*a*, *b*) studied Sahelian savannah in Senegal, Josens (1971*a*, *b*, 1972) investigated a derived savannah in the moist forest-savannah mosaic area of the Ivory Coast and Wood *et al.* (1977) worked in Guinean savannah in Nigeria. The full details of these studies are as yet unpublished in Doctoral theses and the records of the COPR/ABU Termite Research Team (Wood, Johnson, Ohiagu and Collins) and we are grateful for permission to use much of this information.

Populations of mound-building termites in all three investigations were estimated by linear regressions between some measure of mound size and mound population. Matsumoto (1976) adopted the same method for three of the four mound-building species he studied in Malayan rainforest. Lepage (1972, 1974*a*, *b*) and Josens (1971*a*, *b*, 1972) sampled subterranean termites by carefully digging pits to a depth of 50–75 cm and collecting termites as they were encountered. Wood *et al.* (1976) took cores of soil (10 cm diameter) 2 m in depth and extracted termites by a combination of hand-sorting and flotation. Hand-excavation has the disadvantage that termites will escape while the pits are being dug; hand-sorting in the field is notoriously inefficient and there is an unknown proportion of the population below 75 cm. The efficiency of hand-excavated pits has not been tested thus no correction factors can be applied to data obtained in this way. The vertical distribution of the population is indicated by Wood *et al.* (unpublished) who found 25% of the termites at 1.0–2.0 m depth and 7% at 1.75–2.0 m.

The population figures for subterranean termites shown in Table 9.5 are partly underestimated because of the great depth to which some termites penetrate. Vertical distribution varies with species, soil type and season and no general correction factors can be applied.

There is considerable variation in the figures for abundance in natural ecosystems and it is not yet possible to make valid generalisations on the relative population density of termites in major biomes. Maximum populations (4450 per m^2) in rainforest were recorded by Strickland (1944)

Table 9.5. *Abundance and live weight biomass of termites in different ecosystems*

Ecosystem	Species or group of species	Type of nest	No. per m²	g per m²	Author
Warm temperate woodland					
Sclerophyll forest, South Australia	*Nasutitermes exitiosus*	Mound	600	3.0	Lee & Wood, 1971*b*
Semi-arid					
Grassland, North America	*Gnathamitermes tubiformans*	Subterranean (1)	0–9127	0–22.21	Bodine & Ueckert, 1975
		Mean over three years	2139	5.2	
Shrub–grassland, North America	*Heterotermes aureus*	Subterranean (1)	431		Haverty, Nutting & La Fage, 1975
Sahel savannah, West Africa	All species	Subterranean+Mounds (2)	229	1.0	Lepage, 1974*b*
Tropical savannah					
Savannah woodland, North Australia	All species	Subterranean (3)	2000		Lee & Wood, 1971*b*
Grass savannah, Central Africa	*Cubitermes exiguus*	Mound	612–701	1.3–1.9	Hébrant, in Bouillon, 1970
Savannah	*Apicotermes 'gurguliflex'*	Subterranean	70		Bouillon, 1962, 1964
N. Guinea savannah, West Africa	*Trinervitermes geminatus*	Mound	110–2860		Sands, 1965*a*, *b*
S. Guinea savannah, West Africa	All species	Subterranean+Mound (4)	4402	11.1	Wood *et al.*, 1977 and unpublished
Secondary S.G. savannah, West Africa	All species	Subterranean (5)	2966	3.6	Wood *et al.*, 1977
'Derived' savannah, West Africa	All species	Subterranean+Mound (6)	861	1.7	Josens, 1972[a]
Tropical forest					
Semi-deciduous forest, West Africa	All species	Subterranean (5)	3163	8.0	Wood & Johnson, unpublished
Riverine forest, Central Africa	All species	Subterranean+Mound	1000	11.0	Maldague, 1964
Rainforest, West Indies	All species	Subterranean (7)	4450		Strickland, 1944
Rainforest, South America	*Nasutitermes costalis*	Mound	87–104	0.1	Wiegert, 1970
Rainforest, Malaysia	Four species	Mound	1330	3.4	Masumoto, 1976
Agro-Ecosystems					
Grazed pasture, West Africa	All species	Subterranean (5)	2010	2.8	Wood *et al.*, 1977
Maize (first year), West Africa	All species	Subterranean (5)	1553	1.7	Wood *et al.*, 1977
Maize (8–24 years), West Africa	All species	Subterranean (5)	6825	18.9	Wood *et al.*, 1977

Depth of soil samples: (1) 30 cm, (2) 75 cm, (3) 8 cm, (4) 200 cm, (5) 100 cm, (6) 50–60 cm, (7) 7.5 cm.
Sampling methods for subterranean species: hand-excavated pits (Josens, 1972; Lepage, 1974*b*); core samples used in all other studies.
[a] Mean of facies D1 (open savannah woodland) and D2 (moderately open savannah woodland).

from soil cores only 7.5 cm deep which would probably sample less than half of the subterranean population and exclude mound-building and arboreal-nesting species. Mound and arboreal populations of a single species in Puerto Rico, *Nasutitermes costalis* (Holmgren), were estimated as 87–104 per m^2 by Wiegert (1970). In Congo Forest approximately one-third of the mound/subterranean population consisted of mound-building *Cubitermes* (Maldague, 1964) and in Malaysia, Matsumoto (1976) estimated four mound-building species at a density of 1330 per m^2, neither estimate including any arboreal species.

Maximum population densities in savannahs are the same order of magnitude. However, Malaisse, Freson, Goffinet & Malaisse-Mousset (1975), working in Miombo woodland in Zaire, recorded a population density of 15000 per m^2 and biomass of 108 g per m^2 for a single species of *Odontotermes*. These exceptionally high numbers could have arisen from biassed sampling of foraging concentrations and the biomass figure is questionable in view of the data for comparable *Odontotermes* species given in Table 9.6, where the maximum recorded mean individual weight was 3.0 mg. This would give a calculated biomass of 45 g per m^2, a much more realistic, if still high, figure which could be accepted in view of similarly high estimates of *Gnathamitermes tubiformans* (Buckley) from a semi-arid, short-grass, Texas rangeland ecosystem by Bodine & Ueckert (1975).

The latter authors used randomised soil cores 81.1 $cm^2 \times 30.2$ cm and found that monthly populations and biomass fluctuated from zero to a maximum of 9127 per m^2 (22.2 g per m^2). The mean figures over a three-year period were 2139 per m^2 and 5.2 g per m^2, with a fluctuating decline during the study. Clearly, the termites cannot have disappeared completely even though 30 cm cores failed to sample them because an unknown population below this depth remained uncounted. It is implied in this paper though not actually stated, that *G. tubiformans* was the only species encountered since no other species were recorded or even mentioned in passing, but whether or not other species were present, the population density seems to be remarkably high for semi-arid conditions. These studies and the data listed in Tables 9.5 and 9.6, suggest upper limits for termite population and biomass in any ecosystem of around 15000 per m^2 and 50 g per m^2, respectively.

Within the African continent, there are indications (Tables 9.1 and 9.6) that in the succession from dry savannahs to humid rainforest, the number of species increases along with overall abundance and the increasing importance of detritus-feeders at all levels down to soil-feeders. Soil-feeders are absent (or very rare) in Sahel savannah, comprise 3.7% of the numbers (5.9% of biomass) in Guinea savannah, and 11.7% of numbers (9.5% of biomass) in 'derived' savannah. There are no comparable figures

Table 9.6. *Population density, live-weight biomass and respiration of termites in Sahel, southern Guinea and derived savannah in West Africa*

Species	Sahel savannah (Lepage, 1974*a*, *b*)			Southern Guinea savannah (Wood *et al.*, 1977, and unpublished)			Derived savannah (Josens, 1972)[a]		
	No. per m²	g per m²	l O_2 per m² year	No. per m²	g per m²	l O_2 per m² year	No. per m²	g per m²	l O_2 per m² year
RHINOTERMITIDAE									
Psammotermitinae									
Psammotermes hybostoma	105	0.14	0.26	—	—	—	—	—	—
Coptotermitinae									
Coptotermes spp.	6	0.01	0.02	—	—	—	—	—	—
TERMITINAE									
Macrotermitinae									
Ancistrotermes spp.	—	—	—	881	1.59	3.09	268	0.28	0.52
Macrotermes bellicosus	—	—	—	165	0.47[c]	1.90[c]	—	—	—
Macrotermes subhyalinus	39	0.60	1.33	37	0.74	1.72	—	—	—
Microtermes spp.	1	—	—	850	1.02	1.94	149	0.08	0.16
Odontotermes spp.	53	0.12	0.23	260	0.78	1.59	47	0.06	0.12
Pseudacanthotermes militaris	—	—	—	—	—	—	90	0.22	0.44
Apicotermitinae									
Adaiphrotermes sp.[b]	—	—	—	40	0.06	0.12	54	0.04	0.08
Aderitotermes sp.[b]	—	—	—	—	—	—	4	0.01	0.02
Anenteotermes sp.[b]	—	—	—	11	0.02	0.04	—	—	—
Astratotermes sp.[b]	—	—	—	—	—	—	1	—	—
Termitinae									
Amitermes evuncifer	—	—	—	21	0.12	0.25	6	0.04	0.08
Basidentitermes potens[b]	—	—	—	—	—	—	36	0.08	0.16
Cubitermes sp.[b]	—	—	—	104	0.56	1.18	—	—	—
Microcerotermes spp.	3	—	—	1148	1.15	2.21	25	0.02	0.04
Pericapritermes sp.[b]	—	—	—	7	0.02	0.04	—	—	—
Promirotermes holmgreni[b]	—	—	—	—	—	—	6	0.03	0.06
Nasutitermitinae									
Eutermellus sp.[b]	—	—	—	1	—	—	—	—	—
Trinervitermes geminatus	5	0.02	0.04	483	2.27	4.65	158	0.76	1.62
Trinervitermes occidentalis	—	—	—						
Trinervitermes oeconomus	1	—	—				7	0.03	0.06
Trinervitermes togoensis	—	—	—		—	—	13	0.06	0.12
Trinervitermes trinervius	18	0.07	0.15		—	—	3	0.02	0.04
TOTAL	231	0.96	2.03	4008	10.59	22.03	867	1.73	3.58

Respiration calculated from mean weight per individual and weight/respiration regression (see text).
Population density: for sampling details see text.
[a] Mean of facies D1 (open savannah woodland) and D2 (moderately open savannah woodland).
[b] Soil-feeding species.
[c] Estimates by N. M. Collins.

for rainforest, where the abundance of soil-feeders is often self-evident. Although Lepage (1972, 1974*a*, *b*) took account of catenary sequences in Sahel, the observations of Wood *et al.* (1977) and Josens (1971*a*, *b*, 1972) deliberately avoid these. The segregation of soil-feeders into dense concentrations in poorly drained sites in Guinea and Sudan savannahs is well known and the above remarks apply only to the much larger areas of 'typical' savannah.

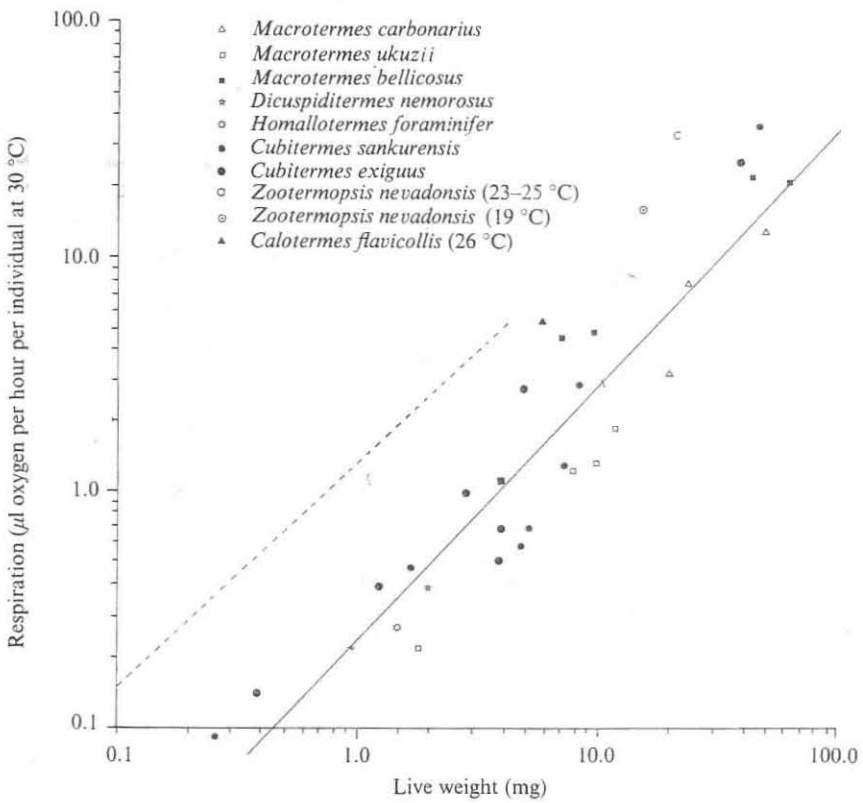

Fig. 9.3. Log–log plot of respiration rate at 30 °C as a function of live weight for different species of termites. Calculated regression line does not include *Calotermes* and *Zootermopsis*. Data for *Cubitermes exiguus* and *C. sankurensis* from Hébrant (1970*a*); *Macrotermes carbonarius*, *Dicuspiditermes nemorosus* and *Homallotermes foraminifer* from Matsumoto (1976); *Zootermopsis nevadensis* at 19 °C and *Kalotermes flavicollis* from Lüscher (1955*b*); *Z. nevadensis* at 23–25 °C from Hungate (1938); *Macrotermes bellicosus* from N. M. Collins (personal communication). Dotted line is log–log relationship obtained by Weigert & Coleman (1970) for respiration of *Nasutitermes costalis* at 21–25 °C as a function of body dry weight.

The influence of cultivation on termite populations in agro-ecosystems has been quantified only by Wood *et al.* (1977, and unpublished), in the southern Guinean savannah of Nigeria. Of the 23 species found in natural woodland, 15 disappeared within one year of clearing and cultivation. After eight or more years mechanical cultivation only four species survived. The reduction in number of species was associated with spectacular increases in *Amitermes evuncifer* Silvestri and *Microtermes* spp., from 20% of a primary woodland population of 4008 per m^2 (Table 9.6) up to 99.9%, in cultivated land, of a population of 6825 per m^2 (Table 9.5).

Respiration

Termites respire in two distinct environments: first, their foraging galleries and runways, where oxygen and carbon dioxide are at similar concentrations to the atmosphere or adjacent soil; second, the colony hive, where both temperature and carbon dioxide concentration are raised (Ruelle, 1964; Lee & Wood, 1971*b*). The methods and general problems of measuring respiration rate in ants and termites are reviewed by Peakin & Josens in Chapter 6 of this volume.

By assuming a respiratory quotient (RQ) of 1.0 (Lüscher, 1955 obtained values of 0.9 for *Zootermopsis nevadensis* (Hagen) and *Calotermes flavicollis* (Fabr.)) we have calculated a regression of oxygen consumption at 30 °C against body weight for various species (Fig. 9.3). The regression obtained (R = respiration in μl oxygen per individual per hour, W = individual weight in mg):

$$\log R = 1.0886 \log W - 0.6578 \quad (P \leqslant 0.01) \tag{9.3}$$

does not include the estimates for *Calotermes* and *Zootermopsis* shown in Fig. 9.3. These species, which are primitive termites having symbiotic intestinal protozoa, appear to have a slightly higher weight-specific respiration rate than the other species, which are all Termitidae. In fact, the Termitidae should probably be divided into taxonomic or behavioural groups, such as fungus-growers, soil-feeders and grass-harvesters, with their own weight-specific respiration relationships (cf. Acari, as shown by Wood & Lawton, 1973).

The slope of 1.09 is at the upper limit of the range (0.6–1.0) for various invertebrates given by Keister & Buck (1964) and is higher than the value of 0.73 obtained by Wiegert (1970) for different castes of *Nasutitermes costalis*. The measurements on *N. costalis* were made at 21–25 °C and the regression

$$\log R = 0.73 \log W + 0.029 \tag{9.4}$$

was obtained on the basis of body dry weight. The respiration is considerably higher than in our calculated regression but would be approximately coincident if calculated on the basis of body live weight (live weight/dry weight = 3.0–4.0; Josens, 1972; Matsumoto, 1976).

Assuming that respiration of 1 l of oxygen results in the release of 20.1 kJ the calculated regression between weight and respiration enables oxygen consumption and respiratory energy loss to be calculated for individual species and for entire termite communities (Tables 9.6, 9.7 and 9.8).

Table 9.7. *Standing crop, production and respiration of different species of termites*

Species	Population standing crop per m²				Production per m² per year[e]				Respiration kJ per m² per year	Production biomass ratios	Production efficiency (%)
					Neuters		Alates				
	No.	g (live weight)	g (dry weight)	kJ[d]	g (dry weight)	kJ[d]	g (dry weight)	kJ[d]			
RHINOTERMITIDAE											
Psammotermes hybostoma[a]	105	0.14	0.033	0.720	0.110	2.394	0.001	0.029	4.81	3.4	33.5
TERMITIDAE											
Macrotermitinae											
Ancistrotermes cavithorax[b]	188	0.20	0.048	0.975	—	9.207	0.024	0.745	7.95	10.2	55.6
Macrotermes subhyalinus[a]	39	0.60	0.096	2.088	0.445	9.684	0.124	3.842	30.89	6.5	30.4
Odontotermes smeathmani[a]	50	0.12	0.033	0.720	0.111	2.415	0.047	1.456	5.27	5.4	42.3
Nasutitermitinae											
Nasutitermes costalis[c]	118	—	0.075	2.331	—	—	—	1.398	22.56	—	—
Trinervitermes geminatus[a]	5	0.02	0.003	0.067	0.006	0.130	0.003	0.088	0.92	3.3	19.1
T. geminatus[b]	158	0.77	0.150	3.022	—	3.139	0.045	1.318	36.16	1.5	—
Trinervitermes trinervius[a]	17	0.07	0.011	0.239	0.018	0.393	0.019	0.557	2.68	3.9	26.2

[a] Lepage (1974*b*).
[b] Josens (1972, 1973).
[c] Wiegert (1970), not including data for eggs.
[d] Calculated from average calorific values (see text): neuters 21.8 kJ per g (dry weight); alates 31.0 kJ per g (dry weight) for Macrotermitinae and 29.3 kJ per g (dry weight) for all other species (Josens, 1972; Matsumoto, 1976).
[e] Calculated from mean weight per individual and relationship between live weight and respiration rate (see text) except for *N. costalis* which was measured directly; combustion of 1 l oxygen is equivalent to 20.1 kJ.

Table 9.8. *Biomass, consumption, production and respiration of termites in three savannah ecosystems in West Africa (data in Table 9.6) and rainforest in Malaysia (after Matsumoto, 1976)*

Ecosystem	Live weight (g per m²)	Annual consumption[b]		Annual production[c] (kJ per m²)	Annual respiration (kJ per m²)
		g per m²	kJ per m²		
Sahel savannah					
Soil feeders	0	0	0	0	0
Macrotermitinae	0.72	15.8	298	24	31
Others	0.24	2.6	49	4	10
Total	0.96	18.4	347	28	41
S. Guinea savannah					
Soil-feeders	0.66	—	136	11	28
Macrotermitinae	6.39	139.9	2635	209	272
Others	3.54	38.7	729	58	143
Total	10.59	178.6	3500	278	443
Derived savannah					
Soil-feeders	0.16	—	33	3	6
Macrotermitinae	0.64	14.0	264	21	25
Others	0.93	10.2	192	15	39
Total	1.73	24.2	489	39	70
Rainforest					
Soil-feeders[a]	1.62	—	—	—	—
Macrotermitinae[a]	1.62	35.5	669	53	72
Others[a]	1.83	20.0	377	30	72
Total	3.55	55.5	1046	83	144

[a] Soil-feeders not studied but many species present; one species of Macrotermitinae and three species of non-Macrotermitinae studied but many other species present (total species = 56; Abe & Matsumoto, personal communication).

[b] Consumption: calculated on basis of calorific value of plant tissue = 18.8 kJ per g; consumption by Macrotermitinae = 60 mg per g per day and by non-Macrotermitinae (i.e. 'others') = 30 mg per g per day; for 'soil-feeders' consumption based on same calorific requirements as other non-Macrotermitinae = 206 kJ per g per year.

[c] Production: based on live weight/dry weight = 4.0 and production:biomass ratio for Macrotermitinae = 6:1 and for soil-feeders and other non-Macrotermitinae = 3:1.

Production

There are two major forms of production in termite colonies, namely alates and neuters. Alates, which are usually produced annually over short periods of time usually during the rainy season, consist of sexually mature males and females with the potential for founding new colonies and represent a loss in biomass and energy to the parent colony. Nutting (1966*a*, *b*, 1969) recorded alates as making up 30% of the total individuals

in *Pterotermes*, 14–16% in *Paraneotermes* and 39% in *Zootermopsis*. Lower values have been recorded for *Trinervitermes geminatus* Wasmann (1–5%: Sands, 1965*b*; Josens, 1972) and *Cubitermes exiguus* Mathot (10%: Bouillon, 1970). Roonwal (1970) recorded 28–43% for *Odontotermes obesus* (Rambur). Because alates are heavier than other castes and have a higher calorific value (Josens, 1972; Matsumoto, 1976: also footnote, Table 9.7) these percentages represent proportionally higher biomass and energy values. Sands (1965*b*) calculated an annual production of 240–470 alates per m^2 for *T. geminatus* in northern Nigeria, which is equivalent to 0.9–1.7 g per m^2. Rowan (1971, quoting a report by Boulton) recorded that a single colony of *Macrotermes falciger* (Gerstäcker) produced 57.2 and 39.0 kg of alates in successive years which even at a postulated low mound density of one per hectare represents a biomass of 3.9–5.7 g per m^2. More detailed quantitative measurements of abundance, live weight, dry weight and production of neuters and alates, taken directly from the works of Josens (1972) and Lepage (1974*b*), are shown in Table 9.7. As far as alate production is concerned there are obvious anomalies in the case of Lepage's (1974*b*) figures for *Macrotermes subhyalinus*, *Odontotermes smeathmani* and *Trinervitermes* spp. which indicate alate production to be greater than or equal to standing crop biomass. This was explained by the author to be due to the fact that measurements of biomass and alate production were obtained independently and that the former was underestimated.

There have been very few measurements of the production of neuters apart from the figures summarised in Table 9.7. The problems associated with making these measurements are fully discussed by Nielsen & Josens in Chapter 3 who give data for *Ancistrotermes cavithorax* (Sjöstedt) and *Trinervitermes geminatus*. With the exception of *Psammotermes*, where alate production was admittedly underestimated, production of neuters is equivalent to that of alates (*Trinervitermes trinervius* (Rambur)) or greater by a factor of two (*T. geminatus*) to four (*M. subhyalinus*). Wiegert's (1970) assumption that the production of neuters approximates to one-third of the biomass is clearly erroneous. The calorific equivalents of production for these species have been calculated using the values given in the footnote to Table 9.7.

The production/biomass ratios in species other than Macrotermitinae are similar to those of other invertebrates (Phillipson, 1973) being approximately 3:1. Macrotermitinae appear to be a special case, having production/biomass ratios ranging from 5.4 to 10.2. These high values appear to be due to the high production of neuters, which may be a response to predation pressure.

The relationship between production and respiration is shown in Fig. 9.4 for the seven species listed in Table 9.7. Although the data are limited

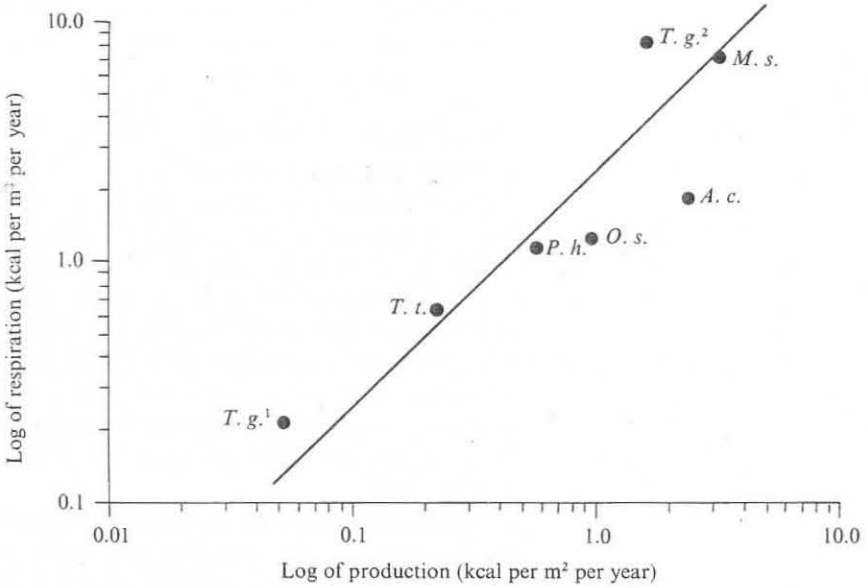

Fig. 9.4. Log–log plot of annual respiration and production for seven species of termites. Data from Table 9.7. The regression line is for a wide range of poikilotherms (McNeill & Lawton, 1970). *T. g.*¹ = *Trinervitermes geminatus* (Lepage, 1974*b*); *T. g.*² = *Trinervitermes geminatus* (Josens, 1972, 1973); *T. t* = *Trinervitermes trinervius*; *P. h.* = *Psammotermes hybostoma*; *O. s.* = *Odontotermes smeathmani*; *A. c.* = *Ancistrotermes cavithorax*; *M. s.* = *Macrotermes subhyalinus*.

there is a good agreement with the regression obtained by McNeill & Lawton (1970) for a wide range of poikilothermic animals.

Net population production efficiency is calculated as $100P/(P+R)$. McNeill & Lawton (1970) divided animals into two major groups: homoiotherms, with production efficiencies of 1.4–1.8% and poikilotherms, with production efficiencies ranging from 20–60%. Termites are within the latter range (Table 9.7) with the exception of *T. geminatus* in the Ivory Coast (Josens, 1972, 1973). Engelmann (1966) suggested that this apparent disadvantage of homoiotherms was possibly offset by the fact that their efficiency of digestion (approximately 70%) was greater than that of invertebrate poikilotherms (30% or less). As indicated in Chapters 4 and 6 of this volume, termites have the advantage of a very efficient digestive system (assimilation efficiency exceeding 60%) and as they also have high population production efficiencies they are ideally poised to convert plant material of one form or another into termite tissue.

We have not yet considered production of saliva. Salivary secretions used for feeding dependent castes are accounted for in alate and neuter production but the saliva used to cement soil particles for building various

structures represents a loss which has not been taken into account. At the present time there are no estimates of the amount of saliva used for this purpose.

Consumption of food and production of faeces

Consumption was discussed in detail in Chapter 4 but there are considerable difficulties in interpreting laboratory and field measurements. Laboratory measurements have the inherent disadvantage of being unrealistic, particularly for social insects. On the other hand, field measurements, if based on removal of either naturally occurring or artificially provided substrates, have the disadvantage that some termites feed on a wide range of substrates in different situations and it is difficult to measure all the variables. For example, *Odontotermes smeathmani* in savannah woodland in Nigeria feeds predominately on woody litter but also on tree bark, grass litter, dung, to a small extent on leaf litter and probably on subterranean woody roots.

With these reservations and using data provided in Tables 4.1 and 4.2 of Chapter 4, this volume, we have adopted mean weight-specific consumption rates of 30 mg per g live weight per day for other sub-families and 60 mg per g live weight per day for Macrotermitinae. The latter figure may be an underestimate, as fungal metabolism appears to contribute more to the decomposition of ingested food than does termite metabolism.

Faeces production has been measured gravimetrically for wood-feeding species in laboratory cultures and has been used in conjunction with measurements of consumption to estimate assimilation (Chapter 4, this volume). An average value of 68% for assimilation efficiency will be used in this chapter.

Energetics of termite communities in different ecosystems

Termite communities

The specific parameters of respiration, production and consumption for individual species (Table 9.7) have been combined with population data from three savannah areas in West Africa (Table 9.6) and rainforest in Malaysia (Matsumoto, 1976) to give a preliminary picture of energy flow through termite populations in these ecosystems. The calculated data are shown in Table 9.8 although direct quantitative comparisons between ecosystems are precluded because of deficiencies in the population data. Soil-feeders, Macrotermitinae and species of other sub-families are considered separately. Energy consumption by soil-feeders has been assumed to be similar to that of species other than Macrotermitinae (i.e. 206 kJ per g).

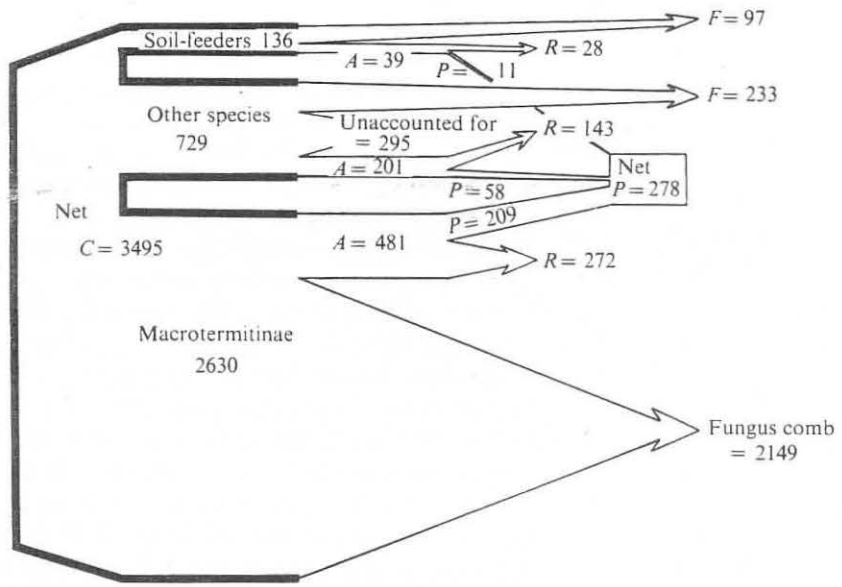

Fig. 9.5. Summary of energy consumption and conversion by termites in southern Guinea savannah; data from Table 9.8. F for 'other species' is based on an average assimilation efficiency of 68% (see text). R = respiration; P = production; A = assimilation; F = faeces production; C = consumption.

The relative importance of the Macrotermitinae in terms of their share of energy consumption appears to be inversely correlated with climatic humidity in West African savannahs (85.9%, 75.3% and 53.9% of the total energy consumed in Sahel, southern Guinea and derived savannah, respectively), whereas the soil-feeders show an opposite trend (0.0%, 3.9% and 6.8%, respectively). There are no data for West African rainforest but in Congo rainforest, Maldague (1964) found a total population of 1000 per m^2 (11.0 g per m^2) of which 337 per m^2 belonged to the soil-feeding species *Cubitermes fungifaber* (Sjöstedt). This species, having a live weight biomass of 10 mg and respiration rate of 2.5 μl oxygen per individual per hour (Fig. 9.3) would have an annual respiratory energy loss of 148 kJ; a value greatly exceeding that of soil-feeders in savannah and approximately equivalent to that of the four dominant mound-builders in Malayan rainforest.

We have attempted to summarise the consumption and conversion of energy for the termite community in southern Guinea savannah (Fig. 9.5), choosing this ecosystem because we believe that it has the most reliable quantitative population data. The most obvious feature is the considerable amount of energy (2.15 MJ per m^2 per year) being metabolised by the fungi in the fungus comb or returning to the ecosystem through decomposition of abandoned fungus combs; decomposition is discussed below and is

thought to be relatively insignificant. There are no measurements of mean annual fungus comb biomass and respiration which enable us to estimate independently the annual respiratory energy loss from fungus combs. G. Rohrman (personal communication) found that oxygen consumption by the fungus comb of *Macrotermes ukuzii* was approximately 120 μl per g wet weight per hour at 30 °C although N. M. Collins (personal communication) showed that the newly deposited comb of *Macrotermes bellicosus* has a much higher respiration rate than older comb. R. A. Johnson (personal communication) has demonstrated seasonal changes in fungus comb biomass of *Microtermes* with a recorded maximum of 27 g dry weight per m^2. Using Rohrman's figure for respiration rate and a value of 50% water content (Roonwal, 1960) of the comb, this latter biomass of *Microtermes* fungus comb would consume 1.14 MJ per m^2 per year of respiratory energy. A second interesting feature is that 295 kJ per m^2 per year of the energy consumed by 'other' species has not been accounted for. This is because faeces production was calculated from consumption on the basis of an assimilation efficiency of 68% (p. 79, Chapter 4) and not by summing production (57.8 kJ per m^2) and respiration (142.7 kJ per m^2) which would have given an obviously low figure of 27.5% for assimilation efficiency ($A = 280.5$ kJ per m^2). Errors in calculations of production and respiration may have contributed to the unaccounted 295.5 kJ per m^2, but it is likely that the anaerobic metabolism of intestinal symbionts, resulting in the release of hydrogen (Hungate, 1939), is a major contributing factor.

The use of average weight-specific rates of consumption, production and respiration to compute energy flow through entire populations is open to criticism unless verified by field data and a comparison of both types of data is shown in Table 9.9. There is good agreement between calculated and measured data for Sahel savannah (Lepage, 1974*b*) but this may be more apparent than realistic as the calculated figures were obtained from population data that are probably underestimated. There is good agreement between calculated and measured data for southern Guinea savannah (Wood *et al.*, 1976, unpublished), where field measurements on wood, leaf and grass litter and their rates of consumption were made independently. However, no field estimates of consumption of bark, arboreal deadwood and subterranean woody roots were made, so that the difference between measured and calculated data may be greater than indicated. In derived savannah (Josens, 1972) the measured rate of consumption is 5.6 times greater than the calculated rate, but the difference should be considerably less as the measured rate of consumption was obtained from short-term baiting experiments which overestimate consumption rate (see Chapter 4, this volume), and there is reason to believe that the population density (and therefore the calculated consumption rate) was underestimated. In rainforest (Matsumoto, 1976) leaf consumption in the field was measured

Table 9.9. *Comparison of estimates of consumption by termite populations (excluding soil-feeders) based on field measurements and on calculation from mean weight-specific rates of consumption*

Ecosystem[a]	g per m²	Consumption by termites (g per m² and as a percentage of available litter)			
		Field Measurements		Calculated data	
		g per m²	% of litter	g per m²	% of litter
Sahel savannah					
Litter production: Total	125	12.5	10.0	18.4	14.7
S. Guinea savannah					
Litter production					
Woody litter	140[b]	86[b]	61.4	—	—
Leaves	230[b]	8[b]	3.5	—	—
Grass	155[c]	98[c]	63.2	—	—
Total	535	192	35.9	179	33.5
Derived savannah					
Litter production: Total	480	135	28.1	24.2	5.0
Rainforest					
Litter production					
Leaves	630	189	30.0	55.5	8.8
Other	430	—	—	—	—
Total	1060	—	—	—	—

[a] See Table 9.8 for authors and calculated data.
[b] N. M. Collins (personal communication)
[c] T. G. Wood & C. E. Ohiagu (unpublished).

by photometrically recording removal, a method which could have included removal by other leaf-eating insects and man, therefore, be an overestimate of consumption by termites.

Oxygen consumption of entire colonies in the field (Hébrant, 1970*a*, *b*; Wiegert, 1970) enables a comparison to be made between estimates of respiration obtained by this means and by the calculated method of multiplying weight-specific respiration rates by population density. Using the first method, Hébrant (1970*b*) obtained a respiration rate of 10.2 ml oxygen per hour for a colony of *Cubitermes exiguus*. On the basis of 650 mounds per hectare (Bouillon, 1970) there is an annual respiratory energy loss of 26.8 kJ per m², compared with calculated estimates of 37.7–72.8 kJ per m². By contrast, Wiegert (1970), found that field measurements of the annual respiration of an average nest of *Nasutitermes costalis* (170 kJ per day) were considerably greater than calculated estimates (74.1 kJ per day). He attributed the difference to the contribution of carbon dioxide liberated by microbial activity in the nest.

No valid comparisons can be made between Lepage's (1974*a*, *b*) field

estimate of production (21.3 kJ per m^2 per year) and the calculated data (27.6 kJ per m^2 per year, Table 9.8) as some of Lepage's measurements (Table 9.7) were used to obtain mean production/biomass ratios which were subsequently used to calculate production.

Comparison with other animals

The significance of termites in ecosystems is well illustrated by comparing their biomass and respiration with that of grazing mammals, as Lee & Wood (1971*b*) did. The maximum biomass of ungulates recorded in a Tanzanian Game reserve by Lamprey (1964) was 12.3–17.5 g per m^2 and their respiration 649 kJ per m^2 per year. The corresponding figures for termites in southern Guinean savannah in Nigeria (Table 9.8) are 10.6 g per m^2 and 442 kJ per m^2 per year, which greatly exceeds the estimate by Child (1974) of 0.7 g per m^2 for above-ground mammalian biomass in a nearby game reserve, although this was in the less productive northern Guinean savannah.

In Senegal at the IBP Sahel savannah site of Fété Olé, termite biomass of 0.96 g per m^2 (Table 9.6) exceeded that of all other dominant above-ground arthropods (0.3 g per m^2) and birds (0.3–0.6 g per m^2) but was less than the combined biomass of domestic stock and herbivorous mammals, 2.0–3.0 g per m^2 (Lepage, 1974*b*; Bourlière, personal communication).

Mammals may be expected to have a greater weight-specific consumption than most termites, due to their higher metabolic requirements, except when the fauna is dominated by Macrotermitinae which channel much of their consumption into maintaining fungus gardens. There is little information by which consumption by herbivorous termites and mammals can be compared in the same ecosystem. In the Serengeti grasslands, annual grass production of 598 g per m^2 Sinclair (1975) was partitioned among the following: grass-eating mammals (13 species of ungulates, various smaller species) 158 g per m^2 (26.4%); grasshoppers, 46 g per m^2 (7.7%); 'decomposers', 115 g per m^2 (19.2%); fire, 319 g per m^2 (53.3%). In fire-protected grassland grazed by domestic cattle in Nigeria, the total grass production was 316 g per m^2 (Ohiagu & Wood, unpublished). Of this total, cattle consumed 140 g per m^2 (44.3%); grass-harvesting *Trinervitermes* took 8 g per m^2 (2.5%) and 'decomposers' 148 g per m^2 (46.8%). In both of these studies, 'decomposers' included termites, which in the Nigerian grassland were estimated to consume 98 g per m^2 of grass litter (31.0% of grass production).

In the semi-arid Texan rangeland studied by Bodine & Ueckert (1975) the cattle biomass was 5.6 g per m^2, compared with a mean termite biomass over three years of 5.2 g per m^2. The annual mean termite biomass declined during this period from 8.93 (11.51) g per m^2 to 2.80 (3.61) g per m^2, figures for growing seasons only being given in paren-

theses. Laboratory estimates of termite consumption during growing seasons were 41 g per m^2 equivalent to 686 kJ per m^2. Using litter bags, termite consumption was estimated to be 55% surface litter, and 38% litter incorporated in soil. Ungrazed plots treated with chlordane to eliminate termites showed higher standing crops of both grass and litter after 15 months (2227 kg per hectare and 737 kg per hectare, respectively). Ungrazed plots with termites had identical standing crops of grass to grazed plots without termites (1826 kg per hectare and 1829 kg per hectare) but litter in the termite plots was reduced by one-third (to 492 kg per hectare). Litter removal by termites was only slightly lower in grazed plots, but while termites appear to have consumed an equal amount of standing grass (approximately 20% of the standing crop) to cattle when not competing with them, the combined reduction in both grass and litter in grazed plots with termites was less than the sum of reductions in grazed, termite-free and ungrazed, termite-active plots. This suggests that foraging activity by termites might have been reduced by cattle trampling. Termite consumption of grass and litter was approximately 25% of the standing crop in ungrazed conditions, but only about 17% when cattle were present. These figures take no account of grass production stimulated by cropping.

Return of energy and nutrients to the ecosystem

Nutrients and unrespired energy can be returned to the ecosystem through constructional saliva, faeces and termite tissue (Wood, 1976) and the rates and relative importance of these avenues are largely dependent on the feeding habits and social behaviour of the termites. These returns will be discussed largely in relation to energy, carbon and nitrogen and their impact on other organisms.

Return via salivary secretions

We have already indicated that the amounts of saliva used for constructional purposes are unknown but must be considerable, particularly in those species of *Macrotermes* and *Odontotermes* whose mounds comprise several hundred kg per hectare (Lee & Wood, 1971*b*). Saliva incorporated into mounds and other structures is probably utilised by micro-organisms. Boyer (1955, 1959) and Meikeljohn (1965) found that *Macrotermes* mounds (where saliva is the sole cementing medium) contained a considerably greater number of micro-organisms than surrounding soils but nothing is known of their contribution to decomposition of saliva.

Returns via faeces

The chemical composition of faeces has already been discussed briefly above and in more detail by Lee & Wood (1971*a*, *b*), largely in relation to species feeding on grass and wood. Little is known of the properties of the faeces of soil-feeding species. The chemical and physical properties of faeces and their distribution in the form of gallery linings, structures in which they are incorporated with soil and discrete structures in which they are the dominant component determine their rate of decomposition. The entire nest system, the hive and associated galleries and runways, is maintained and protected against invasion of micro-organisms by intensive nest sanitation and against other invertebrates (with the exception of inquilines) by defensive behaviour. Sands (1969) noted that certain specific saprophytic fungi, particularly species of *Podaxon* and *Xylosphaera*, had been recorded from a wide range of termite nests. They probably have some effect on decomposition of faeces, particularly those species which habitually colonise abandoned fungus combs. However, it appears that the faecal material is not available to other organisms until the nest system, or parts of it are abandoned. Peripheral galleries and runways are abandoned and new ones constructed as food supplies diminish and new ones are exploited, but the hive may be maintained for many years. Estimates of the longevity of colonies range from less than 10 years for *Cubitermes fungifaber* (Noirot, 1970), *Tumulitermes hastilis* and *T. pastinator* (Wiliams, 1968), 30 years for *Amitermes hastatus* (Haviland) (Skaife, 1955), 50 years for *Nasutitermes exitiosus* (Ratcliffe *et al.*, 1952) and more than 80 years for certain *Macrotermes* (Grassé, 1949).

The only available information on decomposition of termite faeces is the work of Lee & Wood (1968, 1971*a*, *b*) on the wood-eating *Nasutitermes exitiosus*. This species builds mounds which are constructed largely of faeces (the internal nursery) or a mixture of soil and faeces (the outer wall surrounding the nursery) which is capped with a thin external layer of soil. When the colony dies the soil capping is rapidly eroded by rain leaving the rest of the mound exposed. A comparison of some of the chemical properties of faecal material in occupied mounds with that in mounds which had been abandoned for 11 years showed that little decomposition of faeces had occurred. This material, which consisted of 42–48% organic carbon, had several properties which undoubtedly contributed to its resistance to decomposition: low pH (3.7–4.1) which would inhibit bacterial activity, high C/N ratio, high lignin (30%) and low carbohydrate (8–10%) content and possibly concentrations of resins, phenols and other resistant wood components resulting from preferential digestion of the more readily degradable components. The C/N ratio in the abandoned mound was high (> 60), although slighly lower than in occupied mounds and the slightly

greater methoxyl content in the abandoned mound indicated that some decomposition of less complex organic materials had occurred with consequent increase in the percentage of lignin. The structure of the outer wall and nursery of the abandoned mound was intact and there were some fungal hyphae, particularly in the basal portion in contact with the soil. The probable fate of the organic matter in these and similar abandoned carton nests is combustion in bush fires.

Further investigations (Lee & Wood, 1971*b*) showed that the microbial population of the outer wall and nursery of occupied and abandoned mounds was very low. Total plate counts of bacteria gave populations ($\times 10^5$ per g dry weight) of 0.06 and 0.12 in the outer wall of occupied and abandoned mounds, respectively and 0.005 and 4.07 for the nursery. There was some colonisation of abandoned mounds by streptomyces ($\times 10^5$ per g dry weight: 0.001 in outer wall and nursery of occupied mounds, 0.35 and 7.0 in abandoned mounds) and to some extent by spore-forming fungi ($\times 10^5$ per g dry weight: 0.02 and 0.006 in the outer wall and nursery of occupied mounds and 0.08 and 1.16 in abandoned mounds). However, these organisms were largely inactive as respiration of samples from the outer wall and nursery of both occupied and abandoned mounds was so low that rates could not be reliably measured.

In addition, Lee & Wood (1971*b*) showed that inhibition of enzyme activity by compounds in the faeces, having properties similar to soil humic acids, may also contribute to inhibition of microbial activity.

Many other termites (Table 9.3) produce faeces with similar properties to those of *Nasutitermes exitiosus* and also construct parts of their nest system largely from faeces. Some of these structures can be expected to have similarly slow rates of decomposition. Others, such as those constructed by *Coptotermes lacteus* (Froggatt) and *C. acinaciformis*, have lower lignin/carbohydrate ratios and appear to decompose more rapidly (Lee & Wood, 1971*b*). There is no information on the decomposition of faecal material used to line walls of subterranean galleries.

The special case of the fungus-growing Macrotermitinae has been discussed in Chapter 4 in relation to utilisation of food and by Wood (1976) in relation to decomposition processes. The entire faecal production of these termites is used to construct fungus combs on which symbiotic *Termitomyces* grow. These apparently convert faeces into assimilable material available to termites which eat the matured parts of the fungus comb. What little is known of the processes involved and the relationships between termites and fungi was summarised by Sands (1969). The net result appears to be complete decomposition of faecal material with no direct return of faeces to the ecosystem, except on the death of the colony. Various organisms, including fungi and other insects, then rapidly break down the comb; these include termites belonging to the genus *Angulitermes*

which specialise in decomposing antelope dung and the abandoned combs of *Macrotermes* (Sands, unpublished). The other exception to the fungus comb cycle occurs in large mounds of *Macrotermes bellicosus* containing fungus combs weighing up to 20 kg, where the fungus comb in a central part of the nest, appears to be inactive and remains uneaten by the termites (N. M. Collins, personal communication). This material would be available for use by other organisms when the *Macrotermes* colony died or became partly colonised by decomposer 'guest' species.

Returns via termite tissue

Direct quantitative comparisons between the three West African savannahs are precluded, because estimates of population density are incomplete or unreliable. However, it is valid to compare, within each ecosystem, the relative returns via faeces and termite tissue. Assuming that there are no faecal returns from Macrotermitinae, and excluding soil-feeders, calculations using the mean assimilation efficiency of 68% and the consumption figures given in Table 9.8 result in returns via faeces of 0.8 g (15.5 kJ) per m^2 in Sahel savannah, 12.4 g (233 kJ) per m^2 in Southern Guinea savannah and 3.3 g (61.5 kJ) per m^2 in derived savannah. Returns via termite tissue are 27.6 kJ per m^2, 277 kJ per m^2 and 38.9 kJ per m^2, respectively, indicating that this avenue of return is more important than faeces in Sahel and southern Guinea savannah but that returns via faeces may be relatively more important in derived savannah. However, the significance of faecal returns is diminished by the loss of an unknown proportion in bushfires and the fact that their nitrogen content (0.5%) is 11–25 times less than that of termite tissue (5.6–12.6%; Matsumoto, 1976). It is probably only in certain rainforests where soil-feeders and species building carton-type nests from faeces that returns via faeces are greater than via termite tissue. The latter can be accomplished via decomposition of corpses or predation.

Decomposition of corpses

Oophagy, cannibalism and necrophagy occurs within the colony and has been studied by Dhanarajan (unpublished) in laboratory colonies. In general it is at a low level, apart from oophagy which was estimated by Sands (1965*b*) at 30% in young colonies. When deaths from disease or injury rise in numbers, the corpses are walled off and left to decompose. A few foragers may be lost outside the nest and likewise parts of the annual alate swarms and these decompose if they escape predators. Compared with predation, the returns to the ecosystem through death and decomposition are probably insignificant, apart perhaps from the shed wings of swarming alates, and possibly the exoskeletal elements rejected by small predators, such as ants. Piles of major soldier heads of *Macrotermes*

numbering hundreds are found around exit holes from *Megaponera* colonies.

The predation hazards confronting both neuter castes and alate reproductives that leave their parent colony are enormous. Even those termites that remain in or successfully return to a subterranean refuge are not immune, and the various forms of predation, both opportunist and specialised, are discussed below. Finally we consider a small extra pathway of energy recycling through termitophily and related phenomena.

Predation on alate reproductive colony-founding swarms

This type of predation is entirely opportunistic since the flights are seasonal and cannot provide a regular food supply. Nutting's (1969) review noted that arthropod predators included scorpions, solpugids, spiders, centipedes, dragonflies, cockroaches, mantids, crickets, beetles, flies and wasps. Curiously, ants were not included although Hegh (1922) and Wheeler (1936) discussed predation by ants on termites in some detail. It is likely that ants account for a significant proportion of the probable near-100% mortality of swarming alates. Basalingappa (1970*a*) estimated emergence of *Odontotermes assmuthi* Holmgren at $2.8–3.0 \times 10^4$ from a single hole and recorded *Camponotus* along with predaceous Heteroptera, Diptera and several vetebrates. This author considered colonisation success to be less than 0.5% and even when pairs have successfully dug into the soil they are immediately open to predation by several specialist predators (see below), such as ants of the genera *Paltothyreus* and *Megaponera*.

Vertebrate predators of termite swarms include fish, reptiles, amphibia, birds and mammals including man (Hegh, 1922; Snyder, 1956, 1961, 1968; Nutting, 1969). Of these, the birds are the best documented with varying estimates of the importance of termites in their diets. De Bout (1964) believed that survival of insectivorous palearctic migrants may depend on flights of alate termites. Williamson (1975) produced evidence that the Sahelian zone of West Africa was an important overwintering area for several migratory passerines from Europe and that the breeding populations of these species in Britain had declined during the Sahelian drought which ended in 1973. However, in the Sahel, flights of alates do not start until May which is long after the migrants have departed for their breeding areas in Europe and termite swarms can have little or no effect on their survival. They may, however, be more important to various inter-tropical migrants such as various raptors, rollers and bee-eaters, as Thiollay (1970) estimated that these birds take 10–30% of most swarms. This author distinguished between swarms in savannah that attract hundreds of birds and those in forest which attract small assemblies numbered in tens, and listed 150 species of birds preying on alate swarms, from the large storks

and raptors, to small passerines, many normally frugivorous groups and nocturnal birds such as owls and nightjars. Stomach samples of a roller (*Eurystomus afer* (Latham)) contained up to 800 insects, mostly termites, and large raptors, up to 700 of the large alates of Macrotermitinae.

Thiollay (1970) noted that alate swarms occurred at the start of the breeding season for many tropical-breeding birds and suggested that their high fat and protein content would aid egg formation. Ward (1965) considered that the flight of alates, shortly after the first rains, provided a significant contribution to the diet of certain weaver birds (*Quelea*) in the Sahelian zone of West Africa, as the swarms came at a time when the normal diet of seeds was not available. Ward thought that the high protein content of alate termites would contribute to maturation of gonads and a change to breeding plumage. Net calorific values of alates have been estimated by several authors (Josens, 1972; Matsumoto, 1976; Wiegert, 1970) and average values of 31.3 kJ per g (dry weight) for Macrotermitinae and 29.3 kJ per g for other species have been adopted. Tihon (1946) reported that lightly roasted alates had 36.0% protein and 44.4% fat (dry weight), Cmelik (1969*b*) recorded 47% fat in alates of *Macrotermes falciger*, Basalingappa (1970*b*) recorded 52% and 42% in females and males, respectively, of *Odontotermes assmuthi*. Fox (1966) gave the protein content of alate *Macrotermes* as 18.8% and stated that alate termites had four to five times more fat and minerals than caterpillars and mature locusts. Rowan (1971) reported that the daily calorific requirements of *Passer domesticus* (L.) (mean weight 25 g) was 92 kJ per day, which could be provided by approximately 70 individuals of the average size of *Odontotermes* spp. Ward (1965) found that *Quelea* (mean weight 19 g) consumed an average of 46 alate *Odontotermes smeathmani* per day, a calorific requirement of approximately 59 kJ per bird per day. Lepage (1974*b*) estimated annual alate production by *O. smeathmani* in the Sahel at 1.46 kJ per m^2 (Table 9.7) and indicated that these flights occurred over a period of 31 days. During this time they would be capable of supporting a *Quelea* population of eight per hectare.

Opportunistic predation on foraging sterile castes

Opportunistic predation on neuters is widespread and the predators include all those groups described as attacking alates although the relative importance differs, for example, birds being less important and restricted to species which feed on the ground or arboreally. References and reviews are included in the zoogeographical chapters of Krishna & Weesner (1970), notably Araujo (1970), and in the synoptic works of Hegh (1922) and Snyder (1956, 1961, 1968).

Ants appear to be the dominant opportunistic predators. Sheppe (1970) found that the main opportunist ant predators of 11 species of termites

(predominantly surface foragers including *Hodotermes*, *Trinervitermes* and several Macrotermitinae) in Zambia were *Myrmicaria eumenoides* Gerst. and *Pheidole megacephala* Fabr. Beetles of the genus *Zyas* (Staphylindae) preyed upon *Odontotermes* in the ventilation chimneys of their mound, eating the head and thorax in preference to the abdomen, suggesting that muscle protein was the main item of their diet. Various other arthropods were recorded as predators and in addition termites were observed entrapped in the slime of geoplanid Turbellaria which digested them externally and sucked out the liquified contents through a hole in the abdomen.

Kakaliev & Saparliev (1973) sampled 30 hectares in the 'termite quadrangle' of central Asia, finding 893 'nests' (29.8 per hectare containing 63 individuals per m^2) of *Anacanthotermes ahngerianus* (Jacobson) and recording over 70 species of predaceous ants. The most important ants were the fast-running *Cataglyphis setipes* Em. (3.3 nests per hectare; 2–3 individuals per m^2) and *Cataglyphis altisquamis foreli* Ruzs. (19.2 nests per hectare; 1.9 individuals per m^2). Bouillon (1970) noted that in South Africa the grass-harvesting *Hodotermes* and *Microhodotermes* are attacked by *Anoplolepis custodiens* (Smith) and *Iridomyrmex humilis* (Mayr), respectively to such effect that foraging is limited to an hour or two in any one location. Ohiagu & Wood (1976) observed that although the soldiers of grass-harvesting *Trinervitermes* were able to protect foraging parties against opportunistic ant predators (such as *Iridomyrmex*) when foraging holes were being closed, individual termites were often left 'stranded' on the soil surface and were rapidly consumed by *Iridomyrmex*.

Among vertebrate opportunists attacking the sterile castes, birds and mammals are best documented. Apart from the reviews already mentioned, some recent work has attempted to quantify certain aspects of the habit. Milstein (1964) recorded black and blue korhaann (*Afrotis afra* (L.), *Afrotis caerulescens* (Vieillot)) with 1900 and 1500 workers of *Hodotermes mossambicus* in their respective stomachs. A double-banded courser (*Rhinoptilus africanus* (Temminck)) had 368, and a tawny pipit (*Anthus novaeseelandiae* Vieillot), 34. Saayman (1966) examined stomach contents of *Bubulcus ibis* (L.), *Numida meleagris* (L.), and *Gallus gallus* (L.), finding up to 380 *H. mossambicus* each, equal to 130 kJ, about one-third of their daily energy requirements. Steyn (1967) found as many as 5100 workers of *Hodotermes* in one Guinea fowl (*Numida meleagris*). He estimated their protein content as 10%, fat 12%, equal to 1590 kJ, more than the probable daily requirement. Rowan (1971) stated that termites were used as food by 42.9% of all birds, 38.9% of passerines and 47.3% non-passerines. Aquatic and littoral birds tended to leave them alone, as did a few frugivores and nectar-feeders. Borret & Wilson (1971) found that

18–24% of two species of pipit (*Anthus* spp.) consumed foraging termites. Not all termites are acceptable as food by birds; Roonwal (1970) noted that foraging columns of *Hospitalitermes* (Nasutitermitinae) appeared unpalatable to domestic hens. In northern Ghana the Farafara tribe supply their domestic poultry with *Odontotermes* spp. (mainly *O. smeathmani*) trapped in earthenware pots filled with fresh cattle dung. The pots are inverted on the soil surface, shaded with a leafy branch and after a few days the contents consist more of foraging termites than dung. This and similar practices (Hegh, 1922) have never been quantified.

Many insectivorous mammals take foraging termites. Smithers (1971) examined the gut contents of Botswana mammals and found termites in elephant shrews (*Elephantulus* sp.), the hedgehog (*Erinaceus*, 98% of stomach content of one individual), the vervet monkey (*Cercopithecus*), wild cat (*Felis*), bat-eared fox (*Otocyon*, 26 out of 50 stomachs, mainly *Hodotermes mossambicus*), the cape fox (*Vulpes*, 3 out of 23 stomachs, *H. mossambicus*), the black-banded jackal (*Canis*, 9 out of 59 stomachs, *Macrotermes subhyalinus* and *H. mossambicus*), the side-striped jackal (2 out of 12), the small spotted genet (*Genetta*, 12 out of 78, *M. subhyalinus* 3, *Odontotermes* 1, *H. mossambicus* 7, unidentified 2), the rusty spotted genet (7 out of 30), the suricate (*Suricata*, 2 out of 17), the selous mongoose (*Paracynictis*, 9 out of 34, 6 *H. mossambicus*), the yellow mongoose (16 out of 50, 4 *H. mossambicus*), the white-tailed mongoose (*Ichneumia*), and the dwarf mongoose (*Helogale*, 10 out of 21, 1 *H. mossambicus*, 2 *M. subhyalinus*, 4 *Odontotermes* sp., 3 unidentified). Shcherbina & Sukhinin (1968) gave similar data for a range of vertebrates feeding mainly on *Anacanthotermes* in central Asia.

Clearly, surface-foraging termites, such as the harvester termites which feed in the open, or certain Macrotermitinae, such as *Macrotermes subhyalinus* or *Odontotermes* spp. which feed under thin surface sheets of soil or occasionally in the open, suffer most from opportunistic predation whether this is by ants, birds or mammals. There are no quantitative estimates of consumption by these opportunistic predators.

Specialised predation on foraging sterile castes

The more constantly available food supply represented by the non-reproductive castes has led to the evaluation of behavioural and morphological adaptations to this type of nutrition and in some cases to dependency. Such specialisations have diverged along two pathways to exploit the two main concentrations of termite activity, namely the foraging parties and the brood centre of the colony. The most conspicuous morphological adaptations have arisen in the latter connection, which involves the need for excavation of protective nest walls and resistance to defence mechanisms of the termites themselves. 'Hive' predators,

which are discussed below, also tend to be nomadic since their feeding is commonly destructive, whereas predators on foraging parties require less in the way of digging equipment, but need the ability to harvest rapidly a sufficient amount of food before the rest flees underground. Since they compete with opportunist predators in non-destructive predation their activities tend to be territorial rather than nomadic. Both of these categories include invertebrate and vertebrate predators, and because of their specialisations, there is little overlap between them. Wheeler's (1936) classification of relationships between ants and termites did not take account of this distinction:

(i) *Cleptobiotic*. Ants that steal prey from other ants.

(ii) *Termitalestic*. Ants that live in termite mounds and prey on the brood – e.g. *Centromyrmex* (Ponerinae).

(iii) *Inquilines*. Ants that live in inhabited or abandoned termite mounds and may prey opportunistically on the termites.

(iv) *Termitharpactic*. Ants that habitually raid termites.

His fourth category includes representations of both types of exploitation, and the other groups overlap to a considerable extent.

Specialised, and apparently obligate, invertebrate predators of foraging termites seem to be confined to a few species of Ponerinae (ants). Emerson (1945) and earlier authors recorded concerted raids by *Termitopone commutata* (Roger) on foraging columns of *Syntermes* spp. in South America in which parties of over 100 ants carried off one or two termites each. The African termitophagous ponerine raider, *Megaponera foetens* Fabr., has been known for many years (Hegh, 1922). Fletcher (1973) described recruitment in this species which specialises in attacking foraging groups of Macrotermitinae. Work in progress by C. Longhurst (personal communication) in Nigeria in connection with the COPR/ABU Termite Research Project has shown that the most common target of *M. foetens* is the genus *Odontotermes*, with *Macrotermes* and *Ancistrotermes* used when the preferred genus is not foraging actively. Preliminary estimates of consumption of termites have been made for November 1974, April–May 1975 and October 1975. Expressed as termites per m^2 per day for the two main prey species, they are respectively: *Odontotermes pauperans* (Silvestri) 0.404, 0.855, 0.292; *Macrotermes bellicosus* 0.551, 0.414, 0.246. If this predation continued throughout the year, even at the lowest rates recorded, it would account for well over half of the standing crop biomass of both species in this area of southern Guinea savannah (Table 9.6). Characteristic of these ants is the speed with which a hunting column concentrates its attack on a foraging group of termites; the emergence of 200–300 ants from the nest to their return carrying up to eight termites each may take less than 30 min (C. Longhurst, personal communication; Sheppe, 1970).

The soldiers of Macrotermitinae seem to be ineffective in defending foraging parties against raiding *Megaponera* and therefore these termites are subject to considerable predation pressure in addition to that brought about by opportunistic predators. This may be one reason why Macrotermitinae appear to have a higher production/biomass ratio than other termites (Table 9.8). In contrast, we have noticed that when *M. foetens* encountered a foraging party of *Trinervitermes* the former were repelled and became disorganised.

A parallel type of feeding on foraging termites by a vertebrate was described by Kruuk & Sands (1972). The aardwolf (*Proteles cristatus* Sparrman) specialises almost entirely on those species of *Trinervitermes* that graze in the open at night in short-grass savannahs of East and Central Africa. It appears to locate its prey by scent and hearing and feeds by quickly lapping with a broad adhesive tongue. It runs from one prey location to another, apparently ceasing to feed when the distasteful soldiers predominate in the remainder of the foraging party. In East Africa its principal prey is *Trinervitermes bettonianus* (Sjöstedt) and according to Smithers (1971) *Trinervitermes rhodesiensis* (Sjöstedt) in Central Africa. The aardwolf does not occur in West Africa where the most abundant species of *Trinervitermes* form fast-moving foraging columns rather than grazing swarms covering a large area. Its intake has not been quantified but its 'home range' appears to be 1.5–4.0 km^2. Using a production/biomass ratio of 3:1 for *Trinervitermes*, the annual production by a modest population of 100 *Trinervitermes* per m^2 in an area of this size would supply approximately 21×10^3 MJ per km^2 which is approximately 20–50 times the annual metabolic requirements of a single aardwolf.

Specialised predation on colony brood centres and nest systems

Predation on the brood centre of the colony ('hive', 'mound' or 'nest') has only been perfected on a large scale by a group of invertebrates, the burrowing doryline ants of the genus *Dorylus*. These have entirely subterranean raiding columns and appear to bivouac in the nest systems of the termites on which they prey, but very little seems to be known of their biology. The reaction of termite colonies invaded by *Dorylus* spp. (various 'sub-genera' have been named, but the currently accepted position is to assign subterranean species to this genus, while the surface-raiding species belong to *Anomma* and other genera) varies in different groups. In general, *Macrotermes* spp. seem to stay in their nest systems and fight to a finish, as do *Cubitermes* spp., while *Trinervitermes*, *Pseudacanthotermes* and some soldierless genera such as *Alyscotermes* have been observed to leave their nests and migrate to the surface where the ants do not often follow. Sands (1965*a*) pointed out that *Sociotomie* (Grassé & Noirot, 1951*a*) usually results from *Dorylus* attacks, and Sands (1972*a*)

described a suicidal defensive behaviour in soldierless termites presumably evolved in response to subterranean ant predation. Bodot (1961, 1967*a*) noted that *Macrotermes bellicosus* nests attacked by *Dorylus dentifrons* Wasm. seldom survived, and that this termite appeared to be the preferred prey. In the area of her study in the Ivory Coast, a large proportion of mounds of this species were unoccupied and this was attributed to doryline predation. It also seemed that the dorylines were more active or more successful in environments disturbed by clearing for cultivation, which could be a reflection of the lowered vitality of *M. bellicosus* colonies from shortage of food, or the greater ease of movement for the ants through the loosened soil. *Dorylus* spp. are adapted to penetrate soil spaces, as opposed to digging their own tunnels, and they probably approach a *Macrotermes* colony along the termite's own access galleries more often than by direct entry. The elaborate maze-like structures found in the 'basement' levels of some *Macrotermes* mounds are possibly adaptations against such attacks, although we have found in Nigeria that many dead young mounds bear unmistakable evidence of doryline attack in the ants' mandible marks around the enlarged openings to the queen cell (also recorded by Bodot, 1961, 1967*a*). However, Williams (1959*b*) indicated that *Anomma kohli* Wasm., which is a surface-raiding doryline, was less successful in preying on mounds of *Cubitermes ugandensis* Fuller and *Cubitermes testaceus* Williams, since the ruptured bodies of the workers appeared distasteful and impeded progress towards the brood. The nomadic behaviour of Doryline ants is well known, and is clearly necessitated by their destructive effects on their prey. Several years must pass for a flourishing *Macrotermes* colony to be replaced, and even with the maximum populations of such termites, the distances travelled by foraging *Dorylus* colonies must be considerable.

Vertebrate predators that specialise in digging out termite nests are all mammalian, with typically 'ant-eater' adaptations expressed in varying degrees. They have narrow elongate muzzles, long, adhesive, protrusible tongues, reduced dentition, thick skins, fur, scales, or spines, and powerful fossorial forelimbs and claws. In Africa and India the Pangolins (scaly anteaters, *Manis* spp.) feed on both ants and termites with a preference for the former. The aardvark (*Orycteropus afer* Pallas) of tropical Africa is reputed to be a major predator of termites. However, Smithers (1971) recorded nearly 100% ants in 7 out of 11 stomachs and in only two stomachs did termites constitute nearly 100% of the contents. Other vertebrates specialising in predation on brood centres include the armadillo in Texas (Kalmbach, 1943), ant-eaters (*Myrmecophaga* spp.) in South America (Araujo, 1970), the sloth-bear (*Melursus ursinus* (Shaw)) in India (Sen-Sarma, 1974), the numbat (*Myrmecobius f. fasciatus* Waterhouse) and echidna (*Tachyglossus aculeatus* (Shaw)) in Australia. There are no

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quantitative studies on these specialised vertebrate and invertebrate predators to enable us to gain even very approximate indications of their annual consumption of termites.

Lestobiosis, termitophily and related phenomena

Animals that live in the brood centre or galleries and prey on the inhabitants are a last form of specialised predation which has already been mentioned in connection with ants. Wheeler (1936) defined Termitolestic ants as adapted to this way of life, as exemplified by such genera as *Centromyrmex* and *Carebara*. Lestobiosis is by definition a phenomenon of eu-social organisms, but non-social animals with similar habits (synechthrans) occur in widely separated groups. Here, the borderline with termitophily is not sharp; possibly one evolutionary route to the latter is through the former. Some beetles, such as *Tetralobus* spp. (Elateridae) and *Orthogonius* (Carabidae), are found as larvae or adults in Macrotermitinae mounds and in the absence of other food are assumed to be predatory on the termites. A reduviid bug *Acanthaspis sulcipes* Signoret was recorded by Anwar (1970) as living throughout the year, ovipositing and developing in termite nest galleries (species unspecified), where it was observed to eat two to ten termite workers per hour as a larva, and 15–20 termites per hour as an adult bug.

Lestobiosis and related non-social phenomena have been studied very little and never quantified. The last stage of adaptation, termitophily, was reviewed by Kistner (1969), mainly from the point of view of the staphylinid Coleoptera. As he said, 'Our knowledge of termitophiles is still in the descriptive stage.' This is not the place to continue the review of the extensive literature on the subject especially since there has again been no quantification of the recirculation of termite tissue through this pathway.

We are most grateful to the following research workers who gave us permission to use their unpublished data: N. M. Collins, R. A. Johnson, G. Josens, M. Lepage, C. E. Ohiagu, D. E. Pomeroy and G. Rohrman.